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THE UNIVERSITY OF ALBERTA

REPRODUCTIVE BIOLOGY OF *PICEA MARIANA* (MILL.) BSP. AT TREELINE.

by

© R. ALAN BLACK

A THESIS
SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE
OF DOCTOR OF PHILOSOPHY
IN
PLANT ECOLOGY

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FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled Reproductive Biology Of *Picea mariana* (Mill.) BSP. At Treeline.

submitted by R. Alan Black

in partial fulfilment of the requirements for the degree of Doctor of Philosophy

in plant ecology.

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DATE 6 Oct. '77

ABSTRACT

Macro-mesoclimatic effects on _Picea mariana_ seed production and seedling success were found limiting south of the modern forest line near Inuvik, N.W.T. Germination and survivorship are also affected by microenvironment of a well developed soil hummock terrain. A lower cardinal temperature of 15°C was found important in determining timing and success of germination. Seedling establishment occurred only within 1-8 years after a fire, accentuating the precarious state of treeline.

Field measurements of water relations, when compared to laboratory determinations of leaf water potential vs. net photosynthesis, suggest no water stress related photosynthetic impairment during 1976 for mature trees. Winter measurements of water relations also suggest no water stress. Maximum and minimum leaf water potentials were -7 and -21 bar on 4 August and 1 July, respectively. First year seedlings, demonstrated an inability to control water loss, both in field and laboratory experiments.

Picea mariana dominated vegetation at treeline was described and little change latitudinally was found. All stands were even aged and of fire origin. Growth rates of _P. mariana_ decrease with increasing latitude, and competitive density reductions were found with increasing stand age. A model simulating stand reproduction was constructed and the effects of fire interval on treeline were investigated. Fire intervals, between 80 and 225 years, were not found to affect simulated stand reproduction but shorter or longer intervals reduced simulated reproduction.

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I. INTRODUCTION

In studying the causal factors of species distributions, it has been established that these studies are best carried out near the limits of the distribution. Picea mariana (Mill.)BSP. is of phytogeographic and ecologic interest because of its boreal North America distribution and relative importance as a treeline species.

Previous treeline studies have been of a vegetational (Larsen 1965, 1971a), palynological (Nichols 1975 , Ritchie and Hare 1971) or climatalogical nature (Bryson 1966, Hare and Ritchie 1972, Larsen 1971b). Much speculation on the species interactions was presented in these studies but these speculations were based on a minimum of autecological information concerning the key species involved. These studies operated in a confusing network of terminology which required clarification for this presentation.

Love (1970), based on Hustich (1966), provided the working terminology applied in this study. She divided the northern coniferous vegetation in Canada and Alaska into the Subarctic and Boreal (Taiga) zones. The Subarctic zone ranged from "treeline", the limit of trees regardless of species (Hustich 1966), to "closed boreal forest" or the "economic forest line" (Hustich 1966). Treeline should be separated from species line, which is the limit of one species regardless of growthform (e.g. tree or prostrate shrub). Within the Subarctic zone from treeline to forest line, the "physiognomic forest line" of Hustich, was defined as a broad transitional or "forest-tundra zone". Forest line was generally defined as the limit of forest vegetation covering 50% or more of the landscape. The wide spread forest within the Subarctic zone between the forest line and closed boreal forest was termed the "open boreal forest". Open boreal forest in this study has been used in synonomy with "subarctic woodland" (Rowe 1972), "open woodland" (Hare and Ritchie 1972) and "lichen woodland" (Kershaw 1977).

Associated with the demarcation of these zones has also been a search for the causal mechanisms, among the earliest of which was Halliday and Brown's (1943) correlation of 10°C mean July temperature with treeline. Hopkins (1959), in response to observed discrepancies in this correlation for Alaska, introduced the degree day concept to environmentally separate Alaskan vegetational zones. Bryson (1966) and Larsen (1971b) solidified these correlations with work concerning the frequency of major air mass occurrences and vegetational boundaries. Hare and Ritchie (1972) noted changes in energy budgets and net production associated with the vegetational zones and cautioned that "This relationship works as an interlocking system rather than as a simple control of vegetation by climate; the structure of the vegetation, because of its effect on albedo and aerodynamic roughness, markedly influences climate."

Investigations into causal factors of treeline must also include the effects of past treeline movements which have occurred at varying speeds and irregular intervals from the last proglacial event. Migration of boreal forest tree species to present treeline position began from proglacial positions (14,000 to 15,000 radiocarbon years B.P.) in the United States and southwestern Canada (Whitehead 1973 and Ritchie 1976). These migrating forest species invaded a post-glacial "tundra" (12,900 to 11,600 B.P.) occupied by Betula, Shepherdia and Artemisia in Western Canada (Ritchie and Hare 1971 and Ritchie 1976) similar to the proglacial assemblage described for interior Alaska (Matthews 1974). Forests were probably present (6,200 B.P., Nichols 1975) immediately after deglaciation in the District of Keewatin (8,000 B.P., Bryson et.al. 1969). Ritchie (1976) suggested possible establishment on the stagnant ice and till surface to explain this immediate appearance. These invasions occurred between 11,600 and 8,500 B.P. in the northwest District of Mackenzie with the establishment of a "continuous spruce forest" by 8,500 B.P. on the Tuktoyaktuk peninsula (Ritchie and Hare 1971). This continuous spruce forest remained until 5,500 B.P. near Tuktoyaktuk or 4,800 B.P. in central Keewatin (Nichols 1975) and was believed to be in response to higher summer mean temperatures (+5° and +4±1°C, Ritchie and Hare 1971, Nichols 1976, respectively). Picea, in response to this Hypsithermal climatic change, was probably 300 km north of the modern position in Keewatin and reached the Beaufort Sea in the District of Mackenzie. After 5,500 B.P., Ritchie and Hare report a reduction in tree cover and from 4,000 B.P. to the present dwarf birch-heath tundra has dominated the Tuktoyaktuk peninsula. Nichols (1975) reported a similar but rapid retreat of treeline after 4,800 B.P. and unlike Ritchie and Hare, an advance between 4,500 to 3,500 B.P. Forests subsequently retreated in Keewatin ca 100 km south of modern positions by 2,100 B.P. Amelioration of the climate during the "Little Climatic Optima" about 1,200 to 1,000 B.P. caused an advance of treeline 100 km followed by retreat at 600 B.P. to approximately modern positions.

The differences between Ritchie and Hare and Nichols' regional interpretations for 4,000 B.P. to present, might be an artifact of the sampling interval (2 or 2.5 and 5 cm, Nichols 1975 and Ritchie and Hare 1971, respectively) but was probably due to the location of Ritchie and Hare's sites north of treeline, masking treeline movements to the south. Nichols suggested the possibility of reduced treeline movement in the District of Mackenzie compared to Keewatin.

Nichols also reported the occurrence of "widespread broadly synchronous fires" at 3,500 and 600 B.P. with immediate replacement by tundra vegetation. These observations supported earlier observations and dates for buried soil and charcoal horizons north of modern treeline in the District of Keewatin (Bryson et.al. 1965 and Sorenson et.al. 1971). These fires were believed to be indicative of climatic change, specifically the movement of cool dry arctic air south, and were differentiated from fires after which recovery of forests occurred within 50 years.

Outposts of Picea currently in the forest-tundra zone were generally considered relict from these past advances of forest line (Larsen 1965, Nichols 1976). However, reported invasions of forest-tundra or tundra were found (Griggs 1934, Hansell and Chant 1971, Marr 1948). These observations unfortunately were difficult to interpret or have been re-evaluated in view of increased knowledge of glacial history (see Nichols 1976). Retreat of forest line and apparent destruction of forest during the retreat by fire, posed questions concerning the role of fire. This was further questioned due to the widespread occurrence of burning in closed and open boreal forest (Heinselman 1973, Johnson and Rowe 1975, Rowe and Scotter 1973, Viereck 1973) and somewhat limited burning of tundra and forest-tundra vegetation (Wein 1976).

Disturbances of the vegetation and altered environment for re-establishment of the vegetation (Mackay 1970, Rouse and Kershaw 1971) raised questions concerning the biology of tree establishment in a limiting environment. Environmental limitations have been speculated concerning seed production and seedling establishment of Picea glauca (Nichols 1976) and P. mariana (Larsen 1965, 1974) in North America and other species in Asia (Tikhomirov 1962) but no detailed studies exist.

Dominance of forest line and forest-tundra vegetation in the Lower Mackenzie Valley by P. mariana (Rowe 1972) and reduced importance of Picea glauca and Larix laricina compared to eastern regions adjacent to Hudson Bay (Marr 1948, Ritchie 1959, 1960) raised the question: Why is P. mariana successful at forest line and what are the controlling factors? This question has implications on past distributions of P. mariana and associated environment, but also on vegetational pattern observed by Zoltai and Pettapiece (1974) on a microtopographic scale. These questions were pursued with the knowledge that recent climatic warming during the past two centuries "may have been too small to move the 'seedling treeline' northwards beyond the present woodland-tundra ecotone which was previously established under substantially warmer conditions. Thus, the hypothesis of the historically-established position of some modern treelines implies that a consistently successful establishment of spruce seedlings due to that recent warming should also be searched for within the present northern woodlands, not just in the southern tundra" (Nichols 1976).

This study was undertaken to elucidate autecological factors controlling the limit of P. mariana at treeline and to provide a baseline of information on climatic effects for this species. Autecological factors investigated were: 1) the role of water relations and photosynthesis in determining the success of germlings (first season seedlings), seedlings and mature trees; 2) germination potential and production of seed; 3) germination and seedling establishment; 4) growth of seedlings to mature trees; and 5) most important the role of climate and fire interval in the success of the species.

II. SITE DESCRIPTIONS

A) Locations

The study areas were located along a north-south transect (ca longitude 133°30') from 40 km north of Inuvik, District of Mackenzie, Northwest Territories (ca latitude 68°40'), to the community of Arctic Red River (ca latitude 67°25'). This 135 km transect was divided *a posteriori* into 4 ecologic regions (Fig. 1) based upon growth and reproductive potential for *P. mariana*. Regions defined on the study transect were approximately 40 km across and encompassed an area within which sampling was considered homogeneous for that region. Access to the area was obtained by helicopter north of Inuvik or along the Dempster Highway for southern sites.

Region I (latitude 68°40' to 68°24') was within the forest-tundra north of continuous forest. Region II (latitude 68°24' to 68°08') was the northernmost limit of open boreal forest and was delimited, based on observed limited growth and reproduction in established vegetation. Regions III and IV (latitudes 68°08' to 67°46' and 67°46' to 67°25', respectively) were regions in which reliable reproduction of stands was recorded in conjunction with generally improved growth rates. Locations of sampling and instrumentation sites within these regions are presented in Table 1.

Figure 1. Map of the study transect. Roman numerals and dashed (---) lines delimit study regions. Dashed and dotted line is the Dempster Highway. Open symbols are instrument sites and closed symbols mark communities.

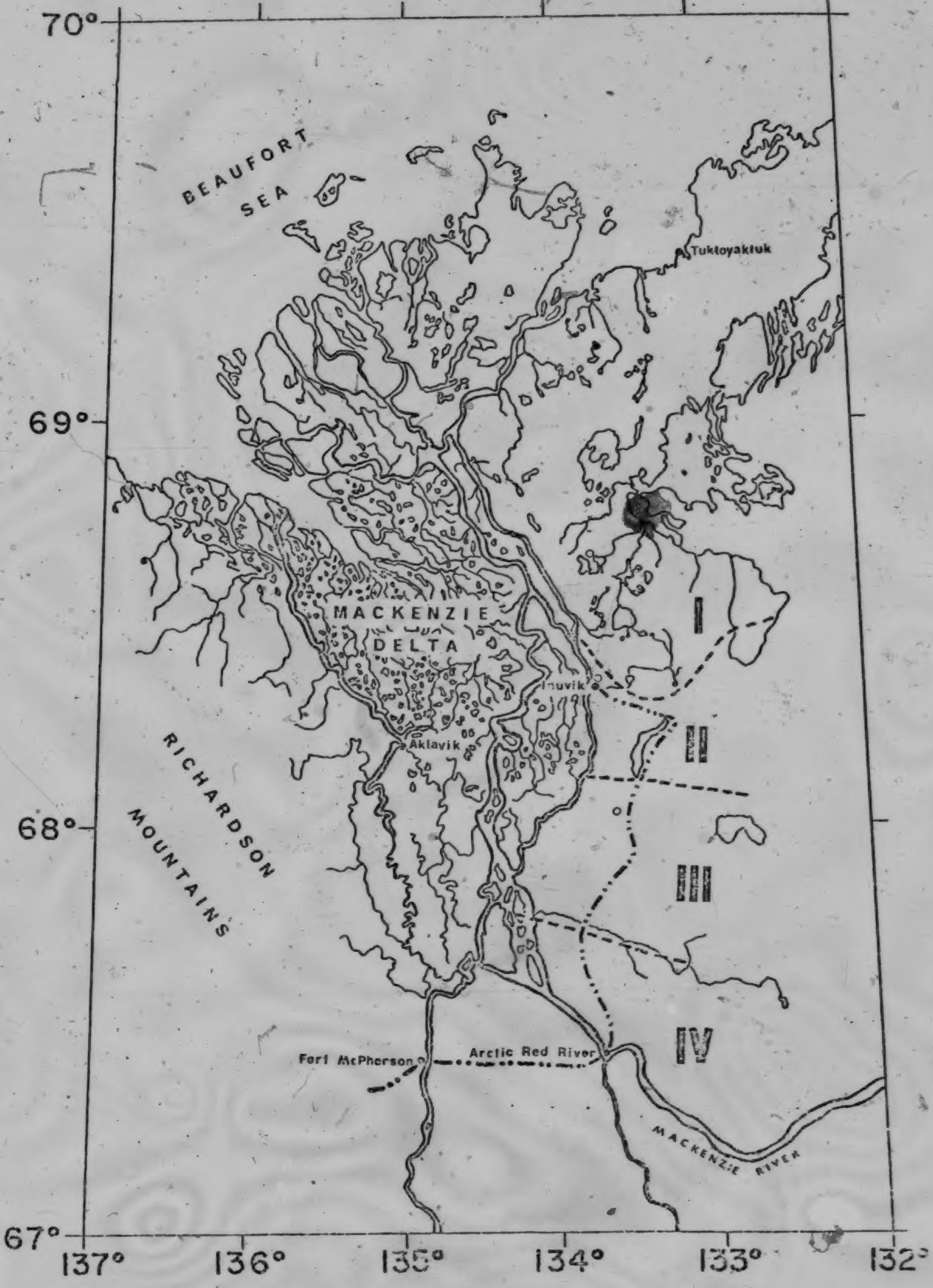

70°
69°
68°
67°
137°
136°
135°
134°
133°
132°
BEAUFORT SEA
Tuktoyaktuk
MACKENZIE DELTA
Inuvik
Aklavik
RICHARDSON MOUNTAINS
I
II
III
IV
Fort McPherson
Arctic Red River
MACKENZIE RIVER

Table 1. Site locations and uses for study transect. Sites shown are instrument, vegetation analysis, burn scar samples and cone and seed production measurement locations.

Site	Latitude/Longitude	Instr.	Veg.	Burn	Cone
Region I					
Ia	68°40'00"/133°27'50"	x	x		
Ib	68°39'52"/133°27'08"		x		
Region II					
N	68°23'41"/133°42'08"	x	x		
IIb	68°23'10"/133°44'37"		x		x
IIc	68°19'00"/133°30'00"		x	x	x
IId	68°18'10"/133°16'25"		x	x	x
IIe	68°14'37"/133°17'08"		x	x	x
IIf	68°14'19"/132°28'54"			x	x
IIg	68°13'14"/133°20'00"			x	x
IIh	68°10'41"/133°25'43"		x	x	
IIi	68°10'41"/133°25'43"			x	x
IIj	68°10'41"/133°25'43"		x		
Region III					
IIIa	68°04'05"/133°28'54"		x	x	x
IIIb	68°03'32"/133°29"37"			x	x
IIIc	68°02'42"/133°28'33"			x	x
IIId	68°02'01"/133°28'12"		x	x	x
IIIe	68°02'01"/133°28'12"		x		
S	68°00'21"/133°28'54"	x	x	x	
IIIg	67°59'03"/133°27'08"			x	x
IIIh	67°55'40"/132°32'42"		x	x	x
IIIi	67°55'40"/132°32'42"		x	x	
IIIj	67°52'50"/133°32'29"		x		
Region IV					
IVa	67°44'30"/134°51'00"		x	x	
IVb	67°37'10"/133°49'16"			x	x
IVc	67°30'32"/133°45'33"		x	x	x
IVd	67°30'32"/133°45'33"		x		

Four types of sites were established in each region; instrumentation, vegetation sampling, burn scar and cone production sites.

Instrumentation sites (2) were located on burns which occurred in Regions I and II (one fire) and in Region III during the summer of 1968 (Heginbottam 1973, Wein 1976). Sites were chosen in upland areas of free drainage where burning had exposed mineral soil and where observed P. mariana reproduction had occurred. These were the intensive meso and microclimatic instrumentation sites and also seed and seedling trial sites. Mesoclimate was used in the sense of general stand climate and microclimate as the climate of microsites or plots on each hummock or representative hummocks. Macroclimate would refer to regional climate either within defined regions or in a general sense for the Inuvik area. An intensive mesoclimatic site (Site Ia) was added during 1976 in Region I.

Representative sites spanning all available age classes were chosen in P. mariana dominated vegetation for all regions. Dominant age classes in Regions II, III and IV were 8, 29, 86, 102, 182 and 250+ years since burning. Only 250+ year-old sites were found in Region I. All sites were restricted to till substrates exhibiting hummocky soil development.

Burn scar sites were chosen in conjunction with vegetation sites and were along burn margins or were isolated trees in otherwise younger vegetation. Trees sampled for cone production were generally felled for stand age determinations.

B) Geology

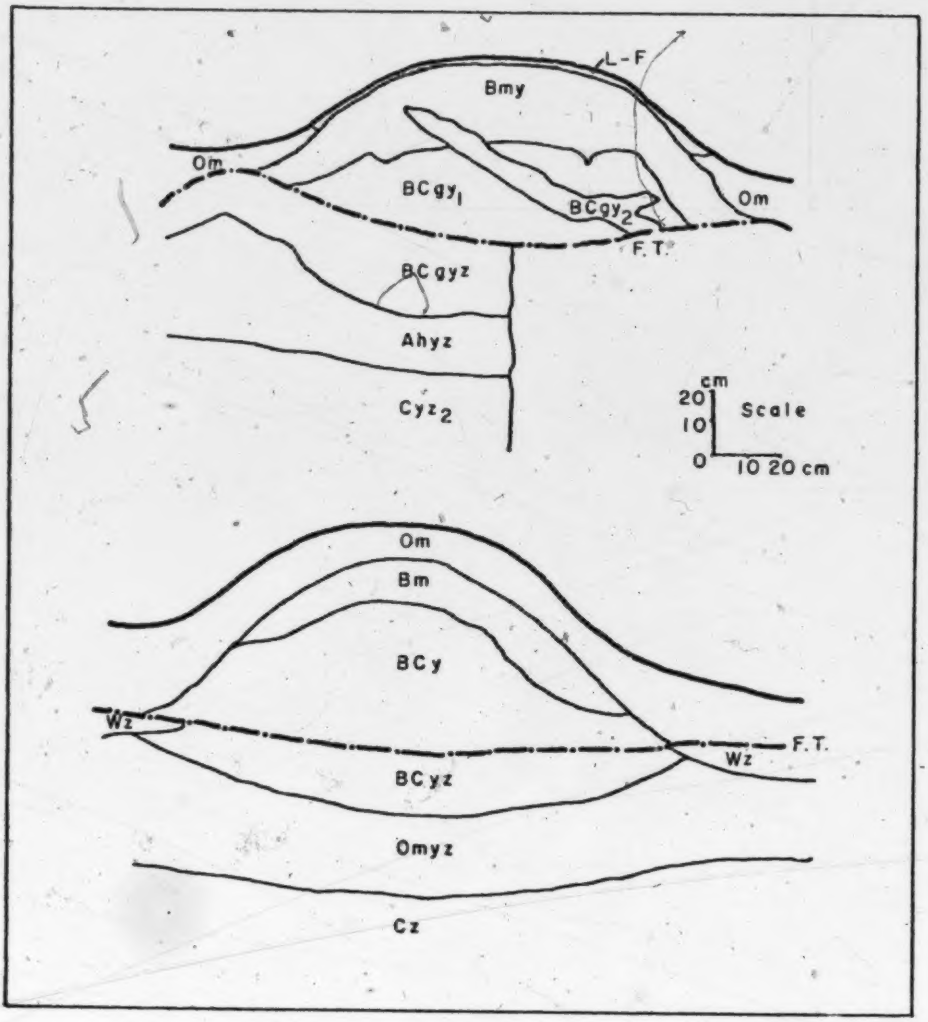
Bedrock geology, of minor importance due to complete Wisconsinian glaciation, changes from unconsolidated Tertiary sands and gravels of the Reindeer formation in Region I to Ordovician-Devonian limestones and dolomitic limestones outcropping in Region II (Monroe 1972). Region III and IV bedrock is composed of undivided shales and sandstones of the Cretaceous or Devonian Imperial formation outcropping only at the Rengleing and Mackenzie Rivers.

Glacial advances during the early-Wisconsinan or possibly pre-Wisconsinan stadials traversed the entire study area reaching into the eastern Richardson Mountains and along the north Yukon coast as far as Herschel Island (Hughes 1972). Late-Wisconsinian advances also probably covered the study area though the positions of terminal moraines are in dispute (Hughes 1972). Deglaciation of the northern sectors, specifically the Tuktoyaktuk peninsula occurred before 12,900±170 radiocarbon years B.P. (Ritchie and Hare 1971), and a minimum ice-free age of 8,200±300 radiocarbon years B.P. was given for the Inuvik area

(Hughes 1972). These glacial events left the region covered with broad morainal plains of low relief (Hughes et al. 1972).

C) Soils

Poor soil development, the result of continuous permafrost and cryoturbation of the fine textured tills, was found associated with P. mariana vegetation throughout the region. The dominant kind of pattern ground found with P. mariana stands was non-sorted circles in Washburn's classification (Washburn 1956) or referred to as Hummocky terrain (Zoltai and Tarnocai 1974). The wide spread distribution of this landform type prompted the addition of the Cryosolic Order (Can. Soil Surv. Comm. 1976) to the Canadian Soil Classification System. This earth hummock form (Fig. 2) is believed to have formed during a past climatic change (Brown 1969), though Zoltai (1975a) has shown that active hummock movement has occurred in the recent past, suggesting a continuous active development. Each hummock consists of a mineral soil core with organic rich horizons above and below of varying thickness. Hummocks also show changing morphologies within a burn cycle (Zoltai and Tarnocai 1974). Post-fire exposure of the mineral soil core, general reduction of the peat cover and blackening of the surface results in melting of ice rich layers and hummock subsidence. Increasing plant and peat covers reverse the


L-F
Bmy
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BCgy$_1$
BCgy$_2$
Om
F.T.
BCgyz
Ahyz
Cyz$_2$
cm
20
10
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Scale
10 20 cm
Om
Bm
BCy
Wz
F.T.
Wz
BCyz
Omyz
Cz

Figure 2. Hummock sections redrawn from Zoltai and Tarnocai (1974). The top section is from the north end of the study transect and the bottom section southeast of Arctic Red River. Soil horizon symbols are after the Canadian Soil Classification System with the addition of y for cryoturbed layers and W indicating greater then 95% water; F.T. designates the frost table. Z indicates frozen horizon.

trend and the active layer decreases in thickness. These changes afford a variety of environmental conditions for post-fire establishment and subsequent plant growth.

D) Climate

Macroclimate of the study area is best categorized as transitional between the Taiga, Continental Tundra and Marine Tundra Climatic Zones (Burns 1973). The transitional nature of the climate results from the interaction of major air masses. Winter months are dominated by Continental Arctic air (cA) over northern Canada which retreats and modifies in summer months to Cold Maritime Arctic (cmA) and Maritime Arctic air (mA). These modified summer air masses are associated with the Beaufort Sea and the stagnant polar ice cap. The frontal formation of these summer air masses (cmA and mA), with Maritime Polar (mP) or rarely Maritime Tropical (mT), air occurs commonly near the study area. Bryson (1966) first associated the northern limits of boreal forest with this frontal pattern and Larsen (1971b) expanded on this thesis. The close proximity of Arctic air masses at all times resultes in cool summers, long cold winters, low precipitation and steep gradients of temperature and precipitation increasing north to south. Macroclimate is summarized for Inuvik in a climadiagram (Fig. 3). Important macroclimatic averages are the 13.3°C July mean and -29.4°C January mean temperatures with 260 mm average annual

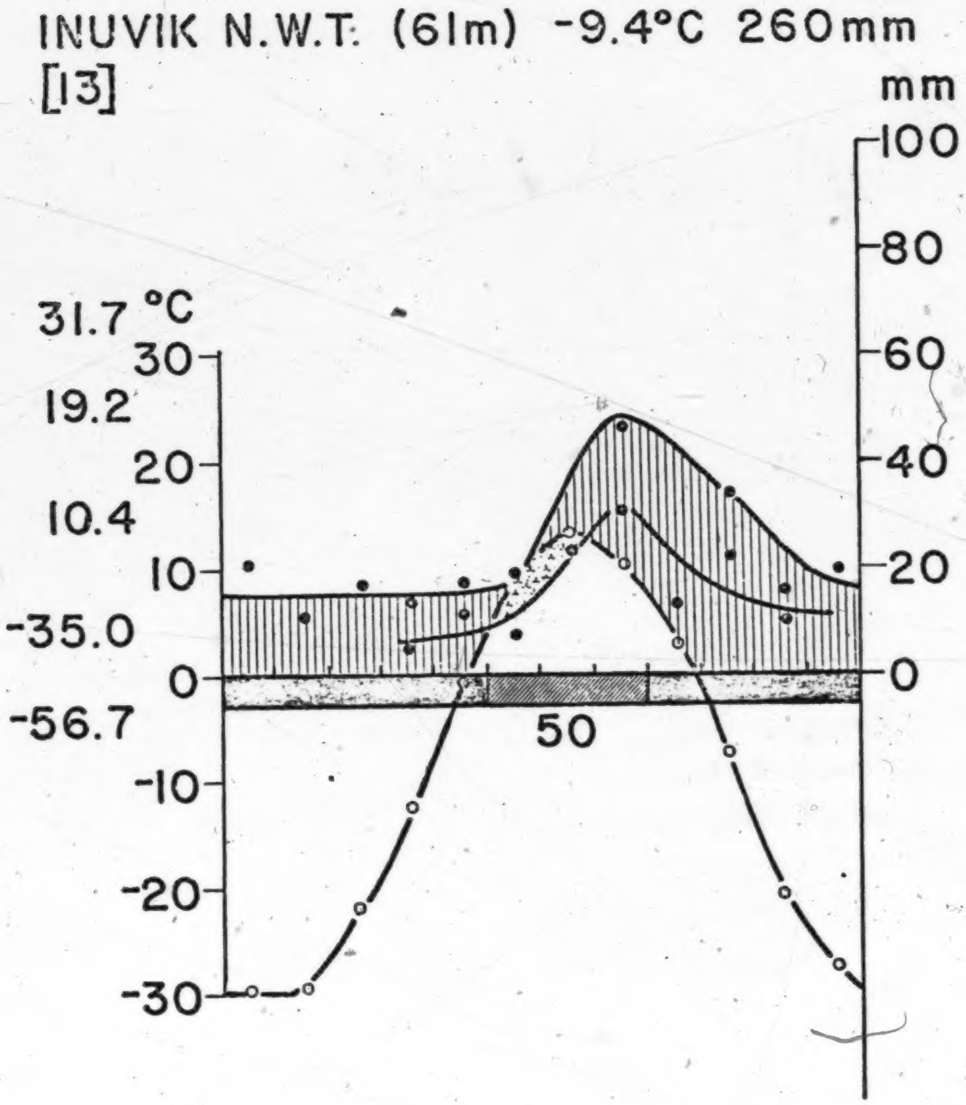

Figure 3. Climadiagram for Inuvik, N.W.T., after Walter (1973). Mean annual temperature -9.4°C; total annual precipitation 260mm; upper line is monthly precipitation; lower line is mean monthly temperature; frost-free growing season is 50 days; solid bar is months with mean minimum temperature below 0°C.; diagonal lines mark months with absolute minimum below 0°C. Vertical bars and hatched area mark relatively humid season and dry period, respectively. Left column of temperatures in descending order; absolute maximum, mean maximum warmest month, mean diurnal temperature range, mean minimum coldest month, absolute minimum.

precipitation of which 67% is received as snow. Snow release (<2.5 cm) generally occurs by 20 May and recordable snow depths (>2.5 cm) generally occur by 10 October.

1. Methods

Meso and microclimates were monitored during summer months in 1975 and 1976 for instrumented sites (Sites N and S) in Regions II and III. Temperature and humidity were measured continuously with a hygrothermograph (Belfort Instrument Co., Model 5-594) housed in a white louvered shelter (Vogel and Johnson 1965) and calibrated at 6 day intervals using a sling psychrometer. Temperature profiles on a representative soil hummock were measured at 1 h intervals using a Grant Model D Multipoint Recorder and thermister probes. Probes with self aspirating shields were installed at +1.5, +0.5, +0.05 top, +0.05 side and +0.05 trough areas of the hummock. Probes were also installed at -0.03 m top, side and trough areas of the same hummock. Supplementary spot readings of temperature every 6 days were made at the surface with an Infrared Thermometer (Barns Engineering Co., Model PRT-10) during 1976 and at -0.05, -0.10 and -0.15 m with thermocouples read with a microvoltmeter and electronic reference junction (Wescor, Inc., Model MJ-55) for both 1975 and 1976.

Wind speeds were measured at 1 m (top of the shrub layer) with a 3-cup totalizing anemometer (Belfort

Instrument Co., Model 5-349). Wind profiles were measured with a hot-wire anemometer (Hastings-Raydist, Model AB-27) and unidirectional probe at +1, +0.5, +0.3, +0.2, +0.1, 0, -0.1 and -0.2 m (0 was the hummock top). Bias in the readings was avoided by recording 10 replicates of readings at 15 s intervals and reporting the mean.

Precipitation was recorded with a wedge type precipitation gauge (Edwards Mfg. Co., Model Tru-Chek) mounted with oriface opening at 50 cm. Evaporation was minimized by the addition of mineral oil to the precipitation gauge.

Soil water was measured gravimetrically at 6 day intervals for surface samples (0 to -2.5 and -2.5 to 5 cm) and water potential equivalent estimated from desorption curves generated by a pressure plate apparatus (Soil Moisture Equipt. Co.). Soil water at -5 and -10 cm was measured with Spanner type thermocouple psychrometers with ceramic cups (Wescore, Inc.) read at 6 day intervals with a microvoltmeter.

Active layer depth was measured monthly at 1 m intervals along a transect with a 1.2 cm diameter rod (n=50), recording also the relative hummock position of each probing.

During 1976, an additional instrumentation site (Site 4) was established in Region I. Hygrothermograph, totalizing anemometer and precipitation gauges were installed and serviced at monthly intervals.

Temperature data reduction consisted of daily maximum, minimum, hourly determined daily mean and maximum-minimum daily mean temperatures. Three day mean, monthly mean and degree day calculations were made using missing data supplied by linear calibrations of Regional sites to the Inuvik airport (Table 3). Precipitation was expressed in 6 day and 3 month totals and wind as monthly averages.

Table 2. Site calibration statistics using 1976 data. Least squares regression using Inuvik airport data are used for missing data.

Site	a	b	r	n
Ia	-0.5209	0.9551	0.9398	65
N	-0.1691	1.0204	0.9768	89
S	2.3739	0.8564	0.9418	70

* a=intercept; b=slope; r=simple correlation coefficient and n=sample size.

2. Results

Mesoclimatic change from Region I to IV, across treeline, was best demonstrated in temperature differences directly affecting length of the growth season. Degree days, above 0°C (Fig. 4), reflected the ca 4°C daily mean

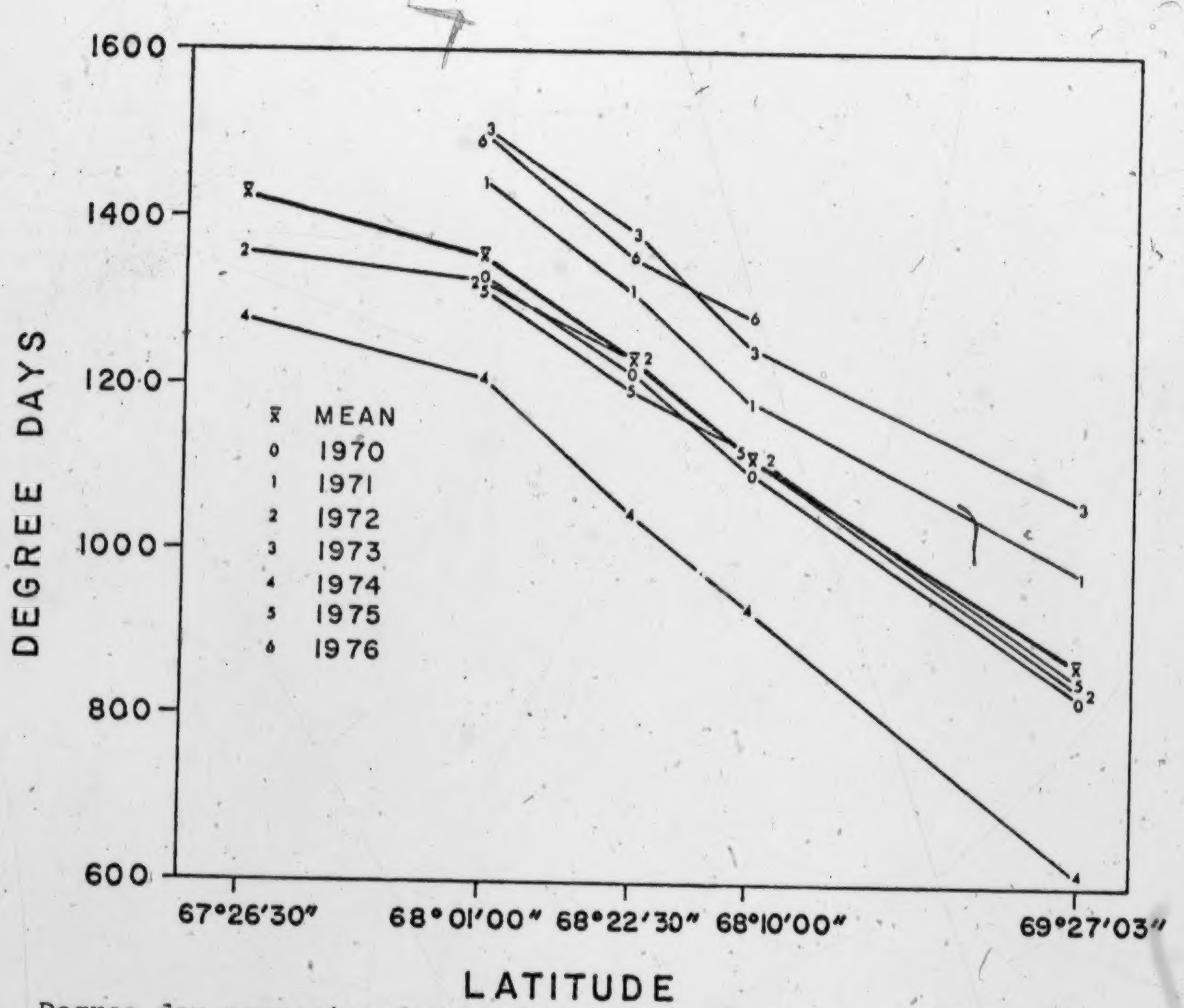

Figure 4. Degree day summaries for study transect for 1970 to 1976 (69°27'03"= Tuktoyaktuk; 68°10'00"=Site Ia; 68°22'30"=Inuvik; 68°01'00"=Site S; 67°26'30"= Ft. McPherson).

difference on the study transect. Distribution of monthly temperatures (Table 3), however, suggested differing conditions in 1975 and 1976 than were apparent in the degree day calculations. 1975 exhibited a much earlier and warmer spring than average and 1976 a cooler than average spring. Degree day summations suggest 1976 was a warmer year primarily due to higher fall temperatures.

Table 3. Monthly site mean temperatures for 1975 and 1976 at study sites and neighboring airports (°C).

	May	Jun	Jul	Aug	Sep
1975					
St N	2.9*	10.6*	13.6	9.7	1.5*
St S	4.9*	11.5*	13.9	10.6	3.8*
Inuvik	3.0	10.6	13.9	10.0	1.7
1976					
St Ia	0.5*	7.9	12.7*	11.7	5.1*
St N	1.0*	8.6	14.0	13.1	5.8*
St S	3.3*	10.3	14.5	12.4	7.4*
Inuvik	1.1	8.9	14.2	12.5	5.9
Means					
Tuktoyaktuk	-4.4	4.4	10.6	8.9	2.2
Inuvik	-0.6	10.0	13.3	10.6	2.8
Ft McPherson	1.7	11.7	15.0	11.7	3.3

*Missing data supplied by site calibrations.

Precipitation did not vary between sites (Table 4) during the two summers, though annual average precipitation

Table 4. June, July and August precipitation summaries for 1975 and 1976 at six northern stations (mm).

	1975	1976	Mean
Tuktoyaktuk	56	48	64
Site Ia	--	92	--
Site N	48*	93	--
Inuvik	77	98	93
Site S	46*	87	--
Ft McPherson	--	--	93

*missing data.

differences exist (129, 260 and 336 mm for Tuktoyuktuk, Inuvik and Ft. McPherson, respectively). Precipitation in 1976 was approximately average for the three-month study period but June precipitation was twice average reflecting the predominance of Arctic air compared to June 1975. Precipitation in 1975 was lower than average.

Humidity (Fig. 5) was relatively constant throughout the summer months, though was lowest and most variable during June and July. This was supported by the climadiagram June and July dry period. The June and July periods of lower humidity were associated with 30-60% higher wind speed (Table 5) than August accentuating these drying effects. Average wind speeds at the Inuvik airport follow the same June to August trends though the absolute values differ, reflecting the 10 m recording height. Wind speed in general decreases 25 to 35% north to south.

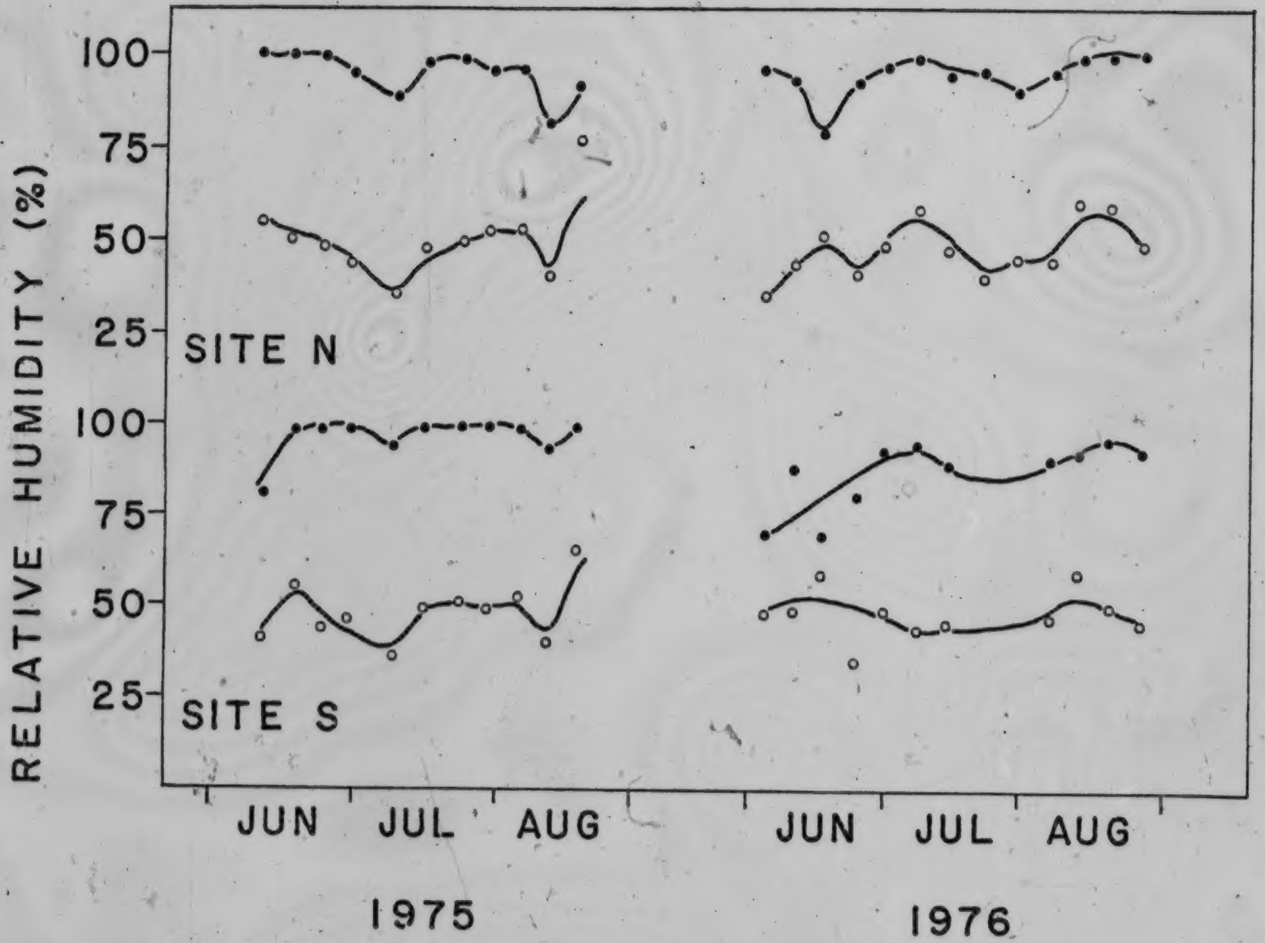

Figure 5. Relative humidities at two instrumented study sites (● =one week mean maximum relative humidity; ○ =one week mean minimum relative humidity).

Table 5. Mean monthly wind speeds for Inuvik airport and study sites, 1975 and 1976 (s^{-1}).

	Site Ia	Site N	Site S	Inuvik	Long term Inuvik mean
1975					
June	---	2.14	1.44*	3.89	3.58
July	---	2.03	1.19	3.89	3.35
August	---	1.85	1.20	3.49	3.26
1976					
June	2.52	2.12	1.56	3.62	
July	1.99	1.85	1.25	3.31	
August	1.81	1.90	1.32	3.49	

*Missing data

Temperature profiles of hummocks (Figs. 6 and 7) suggest earlier spring warming of the hummock top as opposed to peat trough areas (i.e. 3.5, 0 and 1°C for top, side and trough microsite -15 cm temperatures Site N 3 June 1976). This was probably the result of improved drainage and the insulating properties of peat. Higher temperatures and higher wind speeds (Fig. 8) associated with hummock top microsites, grading to lower temperatures and wind speeds in trough areas result in more mesic conditions for plant establishment from hummock top to trough microsites (i.e. Figs. 22, 23 and 24)

Soil water potential at -5 or -10 cm was not measured below -1 bar during 1975 or 1976 in any microsite. Droughty soil conditions, soil water potential below -15 bar, were therefore restricted to surface (0 to -5 cm) layers.

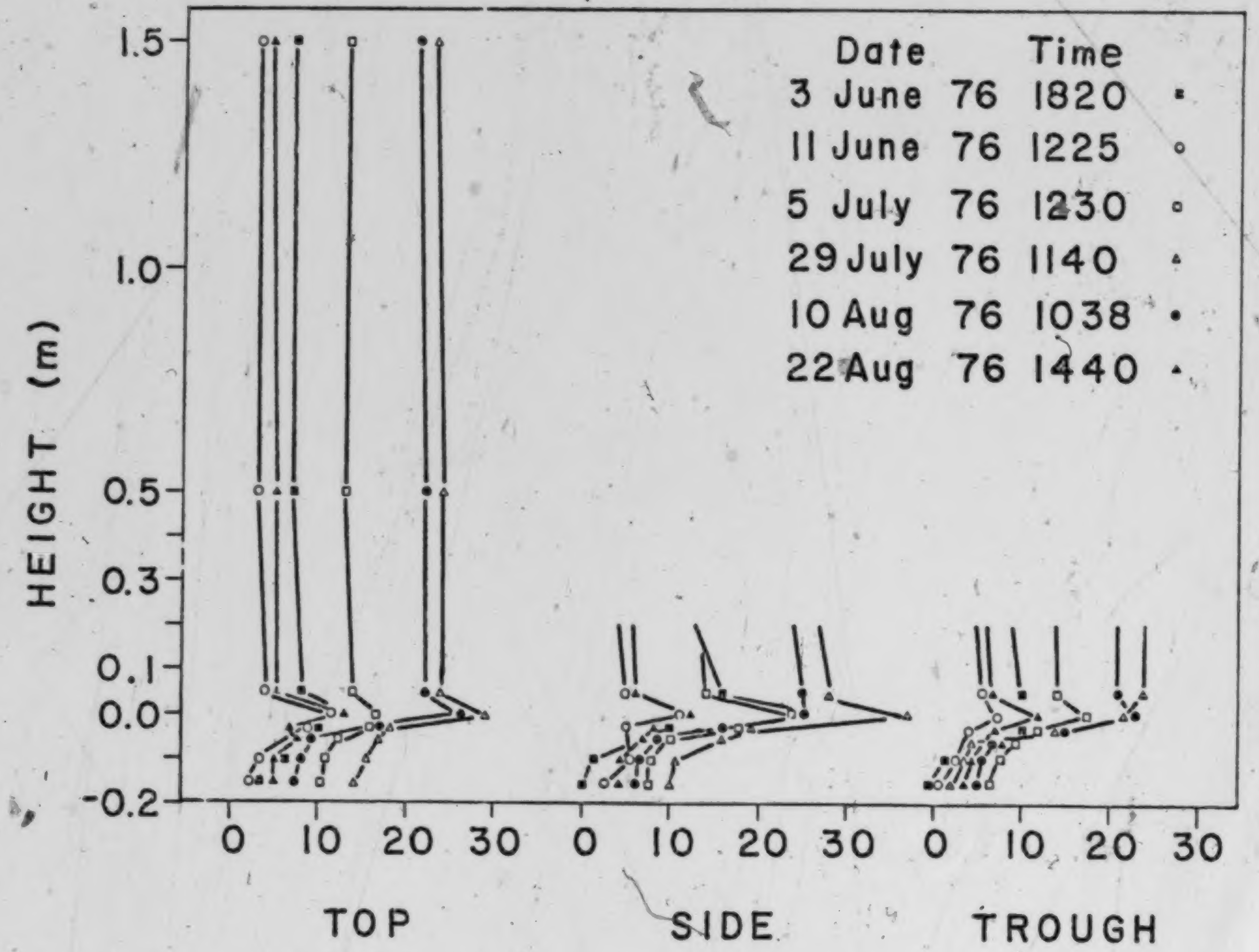

Figure 6. Representative temperature profiles for Site N from the 1976 growing season (°C).

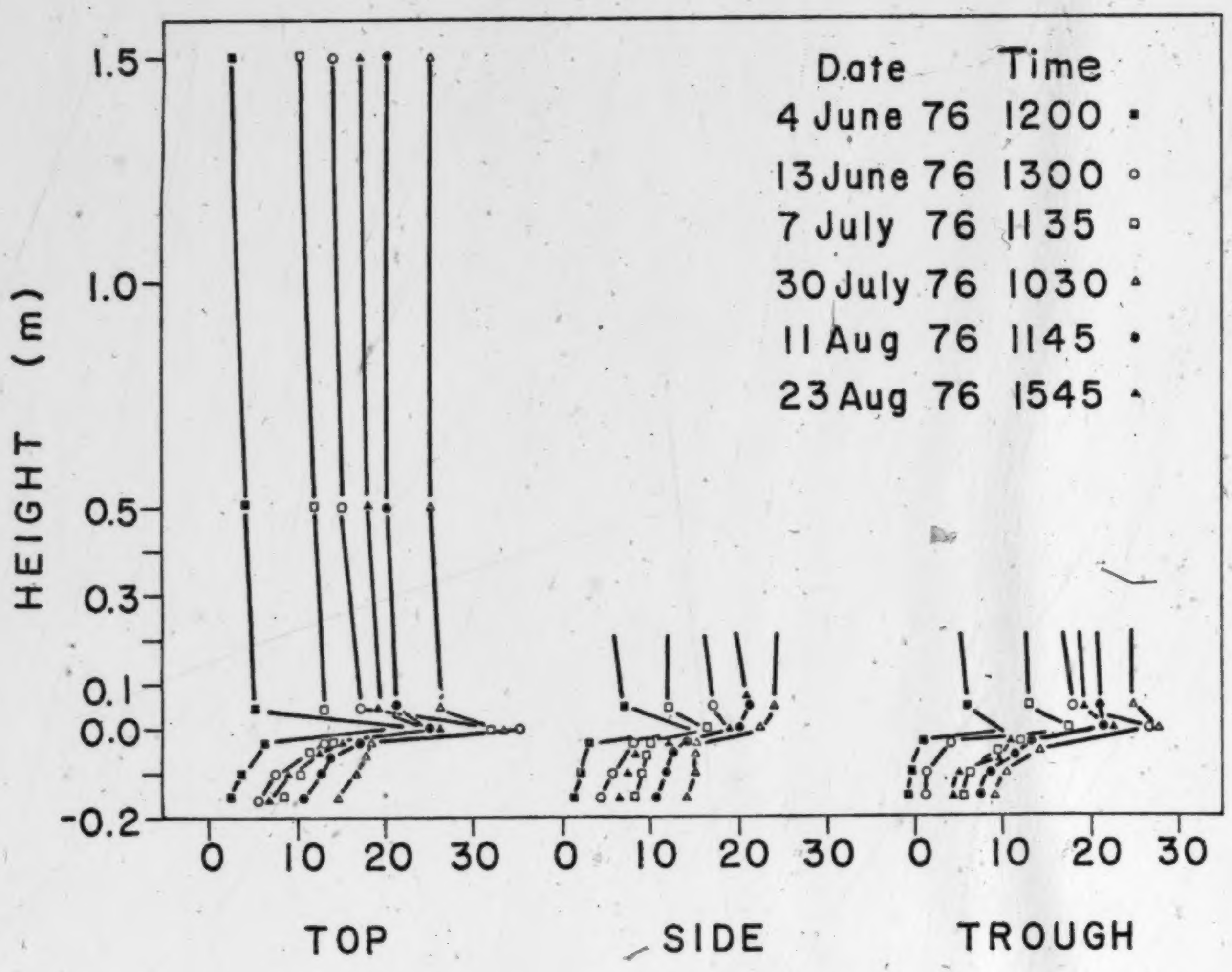

Figure 7. Representative temperature profiles for Site S form the 1976 growing season (^{O}C).

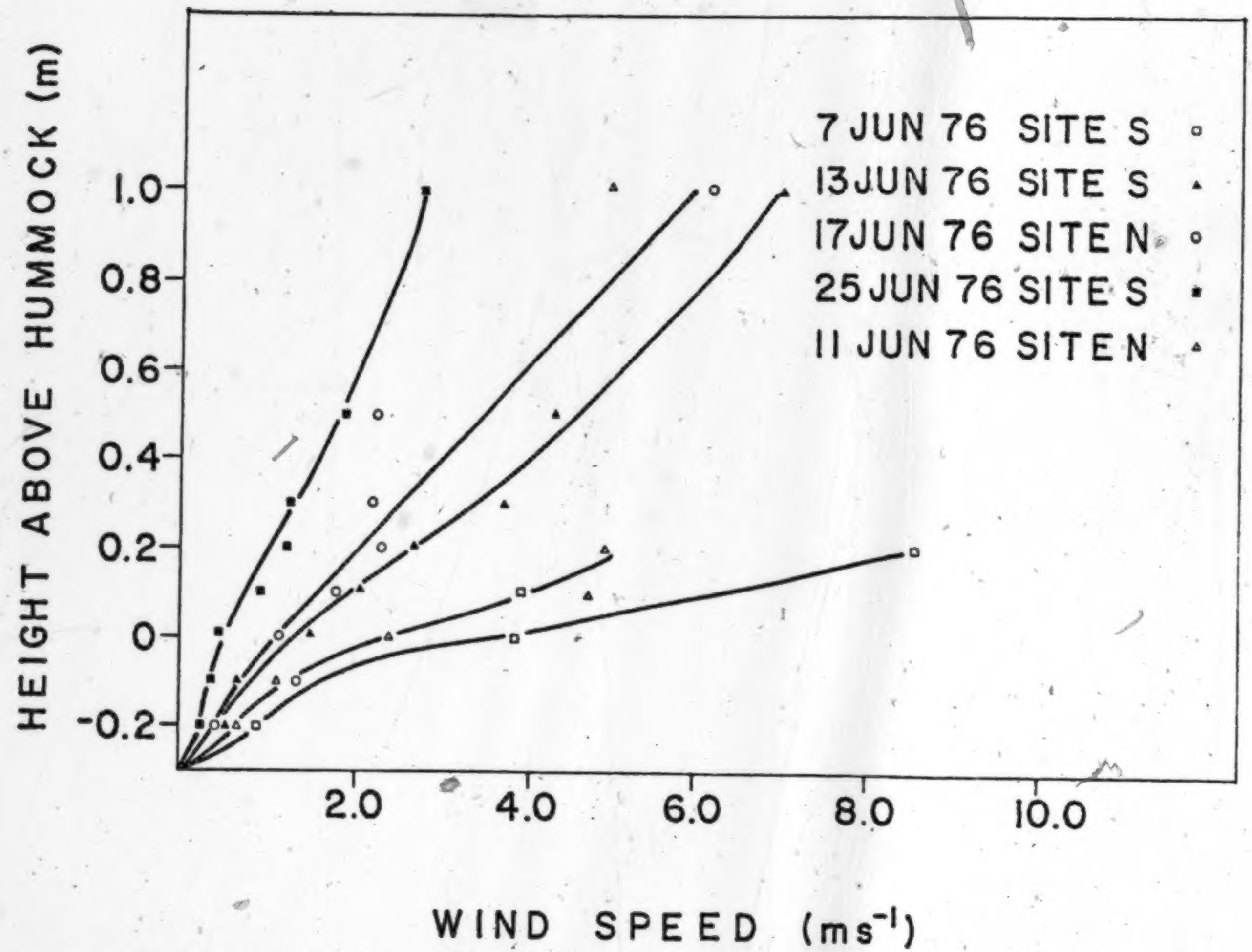

Figure 8. Representative wind profiles from Sites N and S from the 1976 growing season. Zero is the hummock top.

Droughty soil conditions were most common the hummock tops which would have little effect on established plants but profound effects on germinating seed.

Active layer depth of the soil hummocks also reflected seasonal macroclimatic differences between 1975 and 1976 and microclimatic differences (Fig. 9). The hummock core (top) melted deeper and earlier than associated side and trough areas. This resulted from differences in thermal conductivity and latent vs. sensible heat flux of each microsite. Trends in active layer melt in 1975 and 1976 followed spring temperatures with greater June melt in 1975 than 1976. Total active layer depth for all microsites was similar by August in both years.

In summary, gradients in environmental conditions have been examined on two levels, macro-mesoclimate and microclimatic. Macro-mesoclimate changes across the study transect most in daily temperatures during the growing season. Temperature means increase north to south ca 1°C for each study Region, resulting in a vegetational change from self-reproducing forest to forest-tundra and, north of the study area to tundra vegetation. Annual precipitation, though doubling from Tuktoyaktuk to Ft. McPherson, was not markedly increased during the summers of 1975 and 1976 seasons north to south. Microclimate of the hummocky terrain has a considerable effect on vegetation in response to changing environment over relatively short distances.

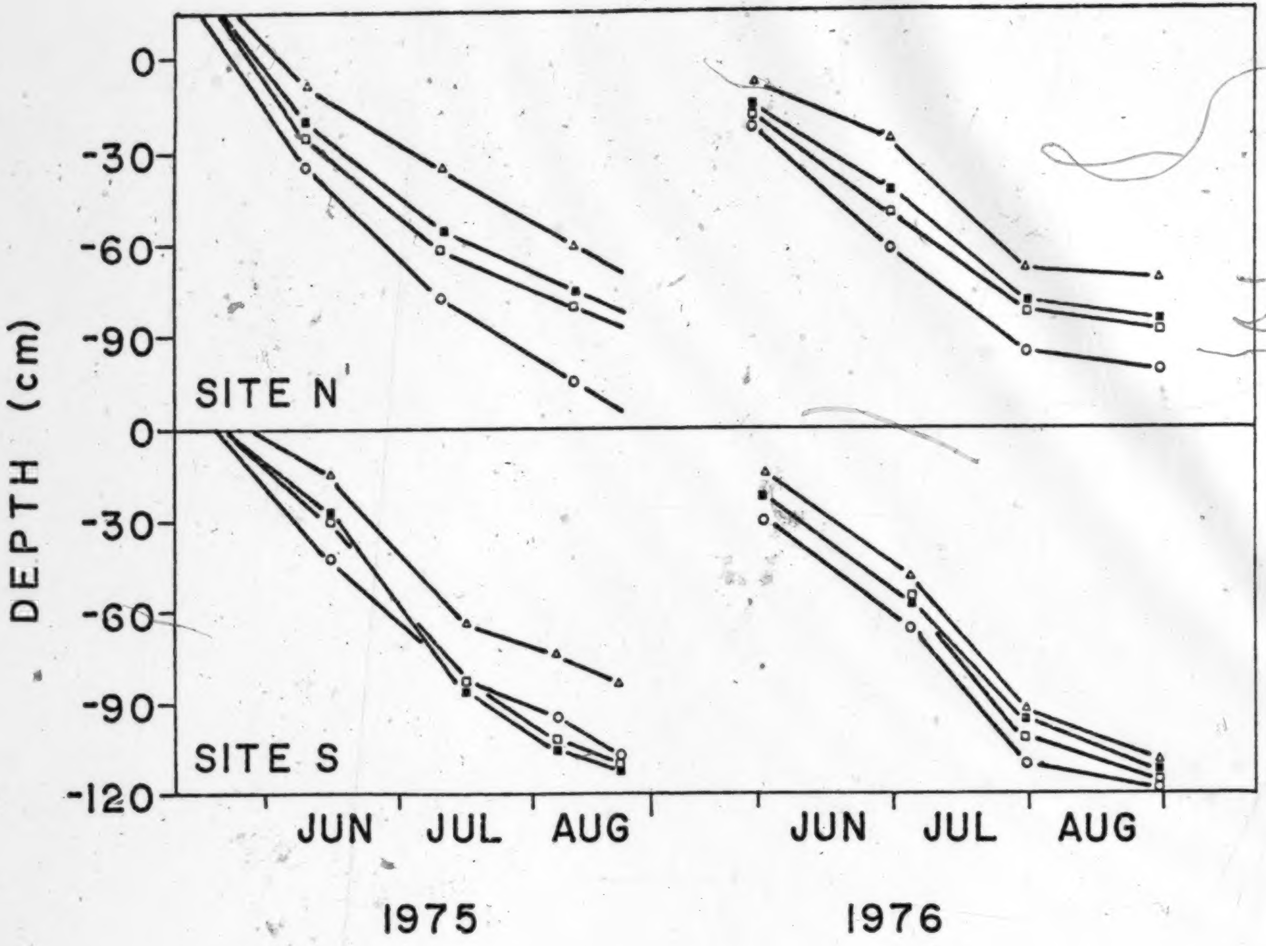

Figure 9. Permafrost depths from Sites N and S (○=top; ■=side; △=trough of hummock; □=mean permafrost depth). Measurement is from the soil surface in each microsite.

Microenvironmental temperature changed as much as 1°C air (+5 cm) and 4 to 5°C soil (-3 cm) from hummock top to trough area but more important snow release and permafrost melt occurred first in hummock top and side microsites. Earlier melt and generally warmer temperatures resulted in droughty soil conditions in hummock top microsites grading to moist hummock trough microsites. In early June, conditions exist with standing water in trough areas and drought conditions on adjacent hummock tops. Vegetation response was most apparent in early stages after burning where hummock tops would be devoid of vegetation but adjacent troughs were covered with luxuriant growths of mosses. These microenvironmental changes will be shown to equally affect _P. mariana_ establishment and success.

III. PHYSIOLOGY

A) Water Relations

1. Methods

All psychrometric determinations of water potential were made using a Spanner type chamber psychrometer (Mayo 1974), and were read with a Wescor MJ55 microvoltmeter after the application of a 10 s (8 mA) cooling current. Psychrometer measurements were made in replicates of three, equilibrated at least 12 hr for total leaf potential and 2 hr for combined osmotic and matric potentials in a room temperature water bath. Data presented were temperature corrected to 25°C (Brown 1970) and were expressed in the standard model of water relations (i.e. total leaf potential is the sum of turgor potential, osmotic potential and matric potential). Combined osmotic and matric potentials were determined after freezing of the original needle sample in liquid nitrogen (-196°c) and turgor was calculated by subtracting combined osmotic and matric potentials from total leaf potential.

Water contents of each psychrometer sample were determined after measurement of combined osmotic and matric potentials. All water contents were expressed as a percent of sample dry weight after oven drying at 80°C. These were the standard techniques for all measurements of water status and only deviations from these techniques will be mentioned below.

Seasonal trends in the water relations of *Picea mariana* were made on three individuals near Inuvik at 6 day intervals during 1976. Samples of the same 5, 3 and 1 m individuals were taken between 1500 and 1800 hr MST on rainless days during summer months to maximize stress measured. Psychrometers were loaded and closed in the field and returned to the laboratory for measurement after a 12 hr equilibration time. Winter samples were transported frozen and sampled under laboratory conditions 1-2 days later.

2. Results

Figure 10 gives the results of seasonal water relations measurements and shows minimum water potentials (=maximum stress) occurring between 13 June and 6 July for all trees, a time of high air and low soil temperatures. Lowest total leaf potential (-21 bars) was measured from the suppressed tree during a period of high air temperature (18°C) July 1. Maximum leaf potentials of -6, -8 and -11 bars for the large, medium and suppressed trees respectively, were measured 4 August and preceded needle cast by these trees (*ca* 10 August).

Combined osmotic and matric potentials show marked increases from -24 to -20 bars beginning on 20 June. These

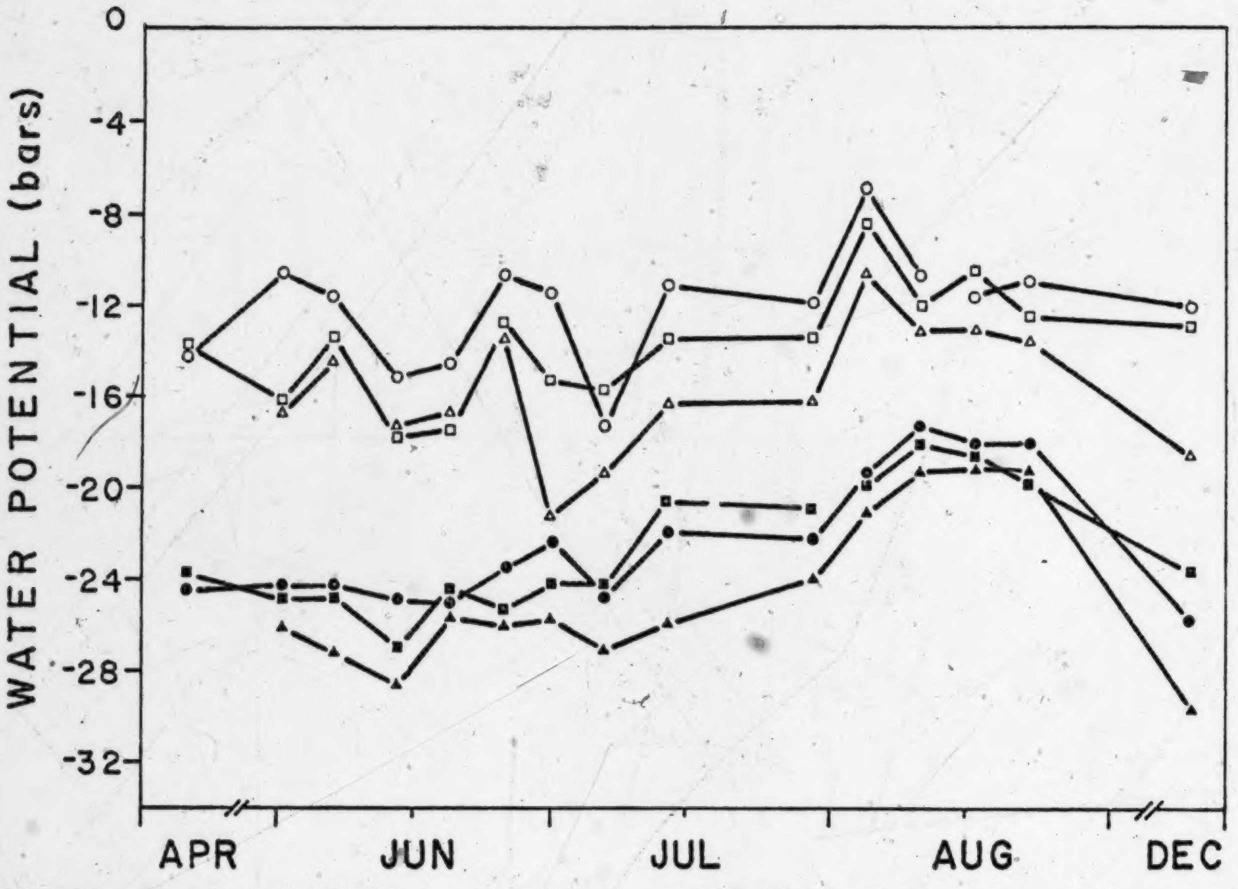

Figure 10. Seasonal trends in water relations of three Picea mariana trees. Total leaf potential is the open symbol and combined osmotic and matric potentials are the closed symbols (○ and ● =5m tree; □ and ■ =3m tree; △ and ▲ =1m tree).

potentials were associated with bud expansion and pollen cast and both events were delayed in the suppressed tree. Combined osmotic and matric potentials decrease with the onset of winter, while total leaf potential remains stable, reflecting a change in water relations associated with winter hardiness. Osmoregulation by the trees maintains turgor constant (10 bars) enabling expansion and growth (Fig. 11). Turgor potential remains stable during the growing season through a range in water contents from 83 to 144%. This osmoregulation results in a significant correlation ($P<0.01$) between water content and total leaf potential for field determinations (Fig. 12).

Germling responses to water stress were investigated in controlled environment chambers (M-12, Environmental Growth Chambers, Chagrin Falls, Ohio) using paired flats of greenhouse mix soil and 10 day old germlings. Temperature (20°C) and illumination (250-300 $uEm^{-2}s^{-1}$ Photosynthetically Active Radiation, PhAR) were held constant. Watering was withheld from the experimental flat and sampling of both the experimental and control germlings occurred simultaneously on a daily increasing to twice daily basis. Each sample consisted of six germlings from each flat for psychronometric readings and water content.

Water potential of the experimental germlings by day 6 had decreased to -10 bars from the control values of -5 bars (Fig. 13). This decrease in water potential resulted in a

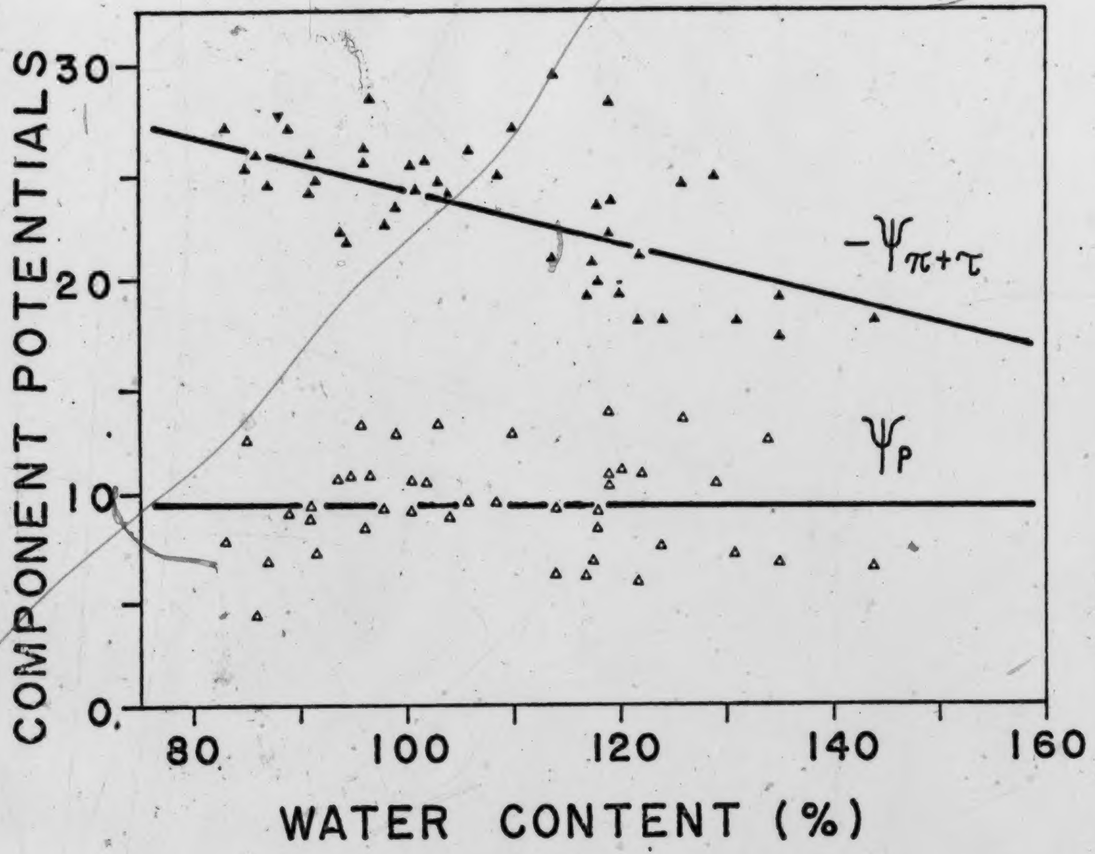

Figure 11. Field measurements of turgor potential and combined osmotic and matric potential plotted as a function of water content (▲=combined osmotic and matric potentials; △=turgor potential).

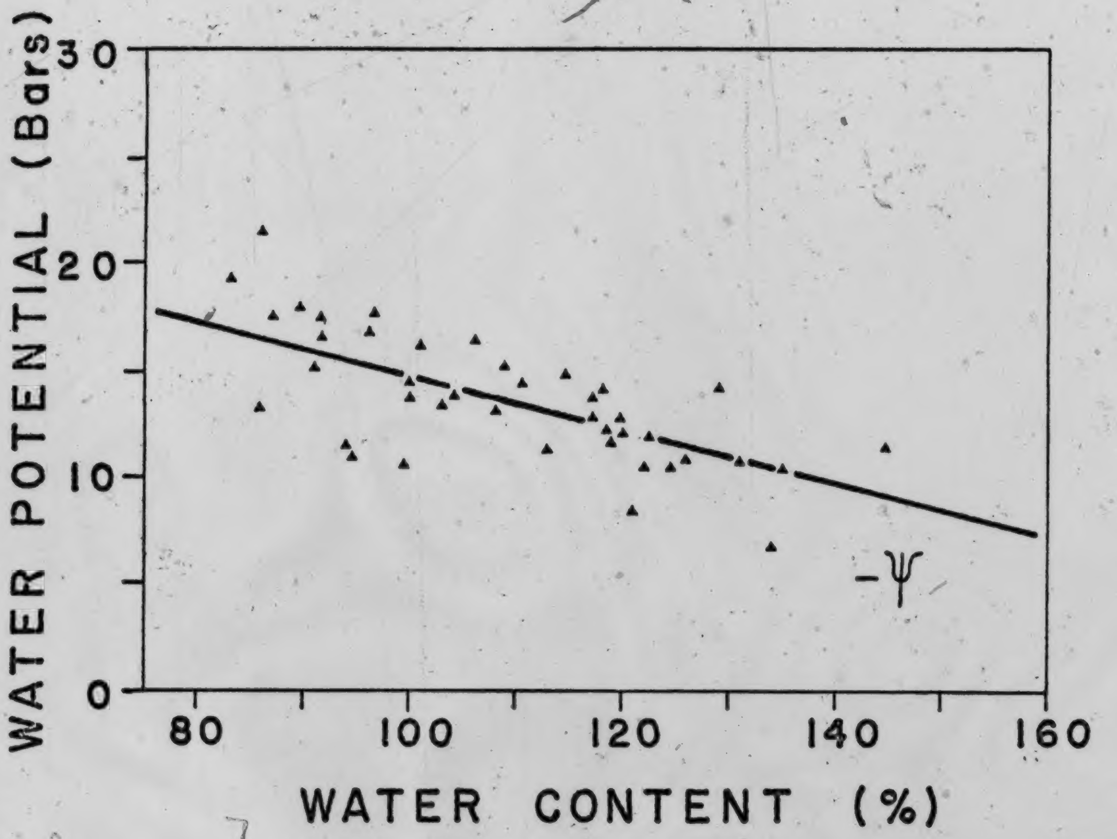

Figure 12. Field measured total water potential as a function of water content from three *Picea mariana* near Inuvik.

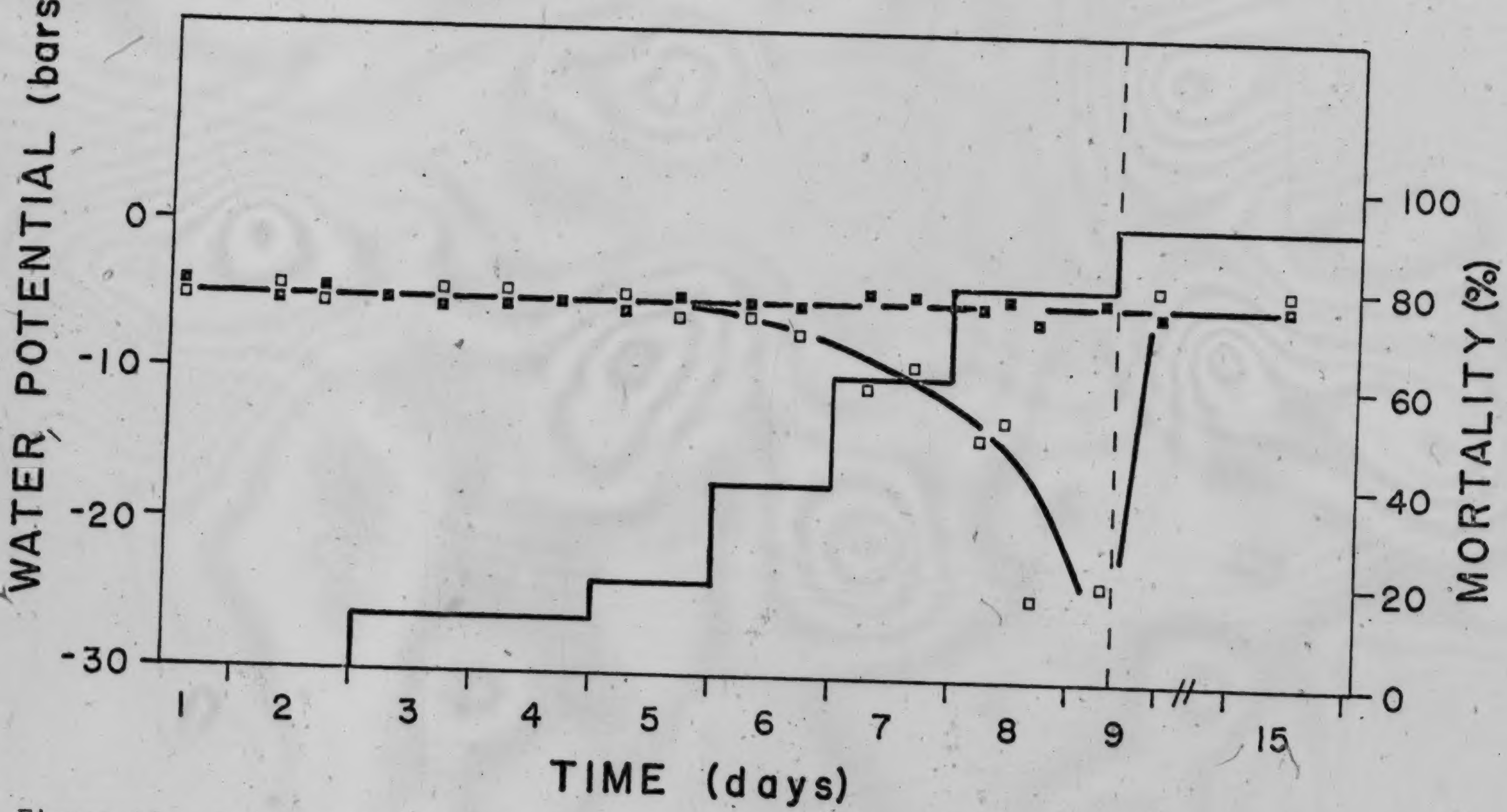

Figure 13. Total water potential and mortality as a function of time since watering. Watering occurred at day 0 and day 9 for the experimental flat of germlings. Mortality is the step function of percent (■ =control germlings; □ =experimental germlings).

60% mortality which increased to 80% with a continuing decreased water potential to -25 bars. No turgor pressure was measured at -25 bars. Recovery after watering of the experimental flat was observed only in individuals which had not wilted during the period of drought. Continued mortality after watering was evident in the 12% additional mortality.

The sensitivity of germlings to water stress is demonstrated in Figure 14. Two points are to be made: first, the decrease in water content of both the control and experimental samples. This is interpreted as maturation of the germlings, the result of an increase in dry weight; second, the water content, which resulted in 0 turgor pressure and -25 bar combined osmotic and matric potentials in the experimental germlings, was not distinguishable from control water contents. This demonstrated that small changes in water content resulted in lethal drops in turgor and combined osmotic and matric potentials.

B) Water Relations and Photosynthesis

1. Methods

Effects of water deficit on rates of net assimilation of carbon (Pnet) were investitigated using four "season" old greenhouse grown P. mariana seedlings. An "open" infrared gas analysis system was used for all gas exchange measurements (Sestak et al. 1971) and in all samples entire

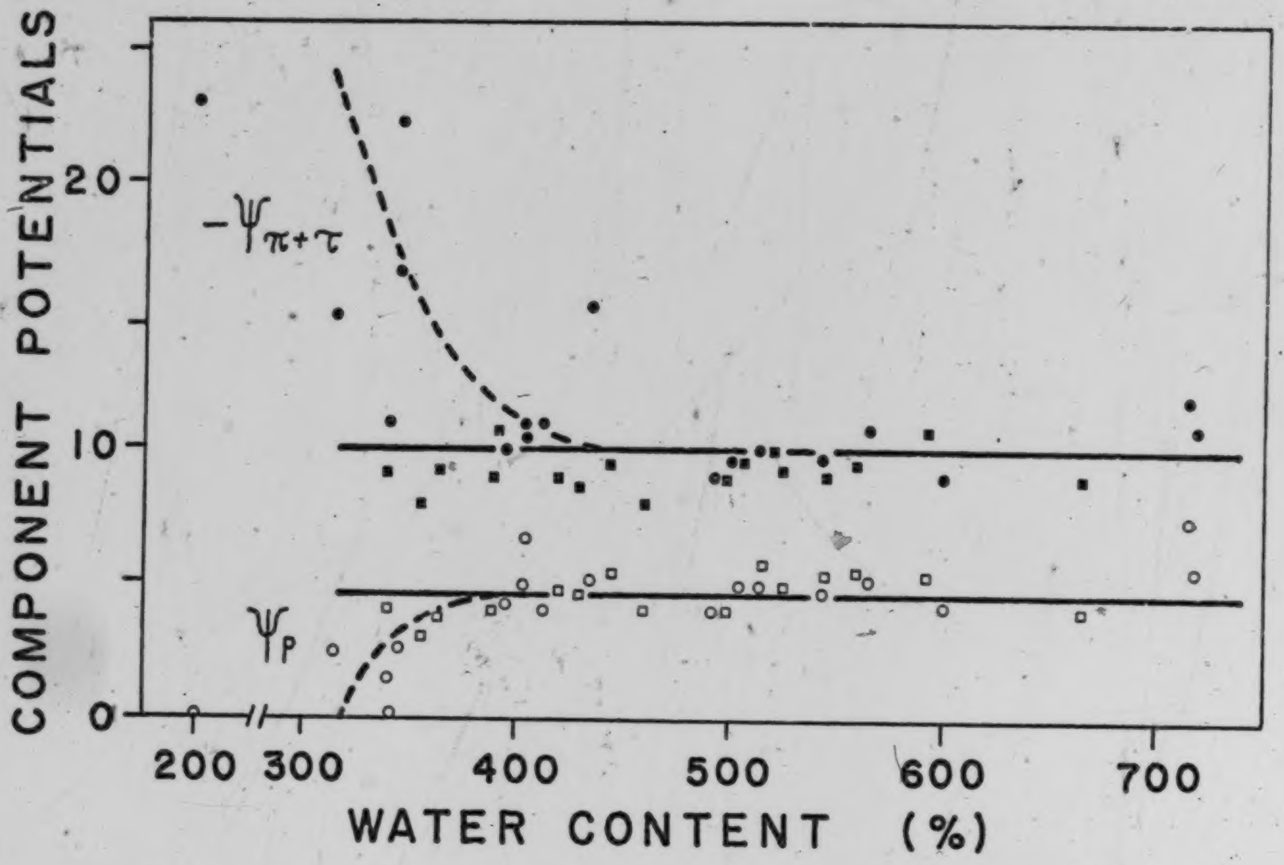

Figure 14. Combined osmotic and matric potentials and turgor potential as a function of water content for germling stress experiment. Round symbols are experimental germlings; square symbols are control germlings; open symbols are turgor potentials; closed symbols are combined osmotic and matric potentials.

seedlings were cuvetted. Differential measurements of gas exchange were determined with a Beckman Model 865 infrared gas analyzer (IRGA) spanned 30 ppm full scale and continuously recorded with a Honeywell 24-channel multipoint recorder. Zero and span of the IRGA were checked using gases standardized after Bate et al. (1969) before each sampling run; gas flow was measured with Gilmont No. 1 flowmeters. Leaf temperature was recorded continuously with leaf thermocouple clips attached to abaxial surfaces. Temperature control of the cuvette was provided by the enclosing controlled environment chamber.

Photosynthetically active radiation was measured continuously using a quantum sensor supplied by Lambda Instruments (Lincoln, Nebraska) connected to the Honeywell recorder. Lighting was provided by the fluorescent tubes in the controlled environment chamber and supplemented by a 1000 watt quartz-iodide lamp which was rheostatically controlled. Two replicate measurements were alternately made using a solenoid switching system (Addison 1977).

2. Results

Descriptive measurements of Pnet for six replicates were made to determine optima for subsequent investigation of stress responses. Temperature optima occurred at 15°C at a constant light intensity of 740 $uEm^{-2}s^{-1}$ (Fig. 15). A broad plateau of responses resulting in Pnet of 1.5

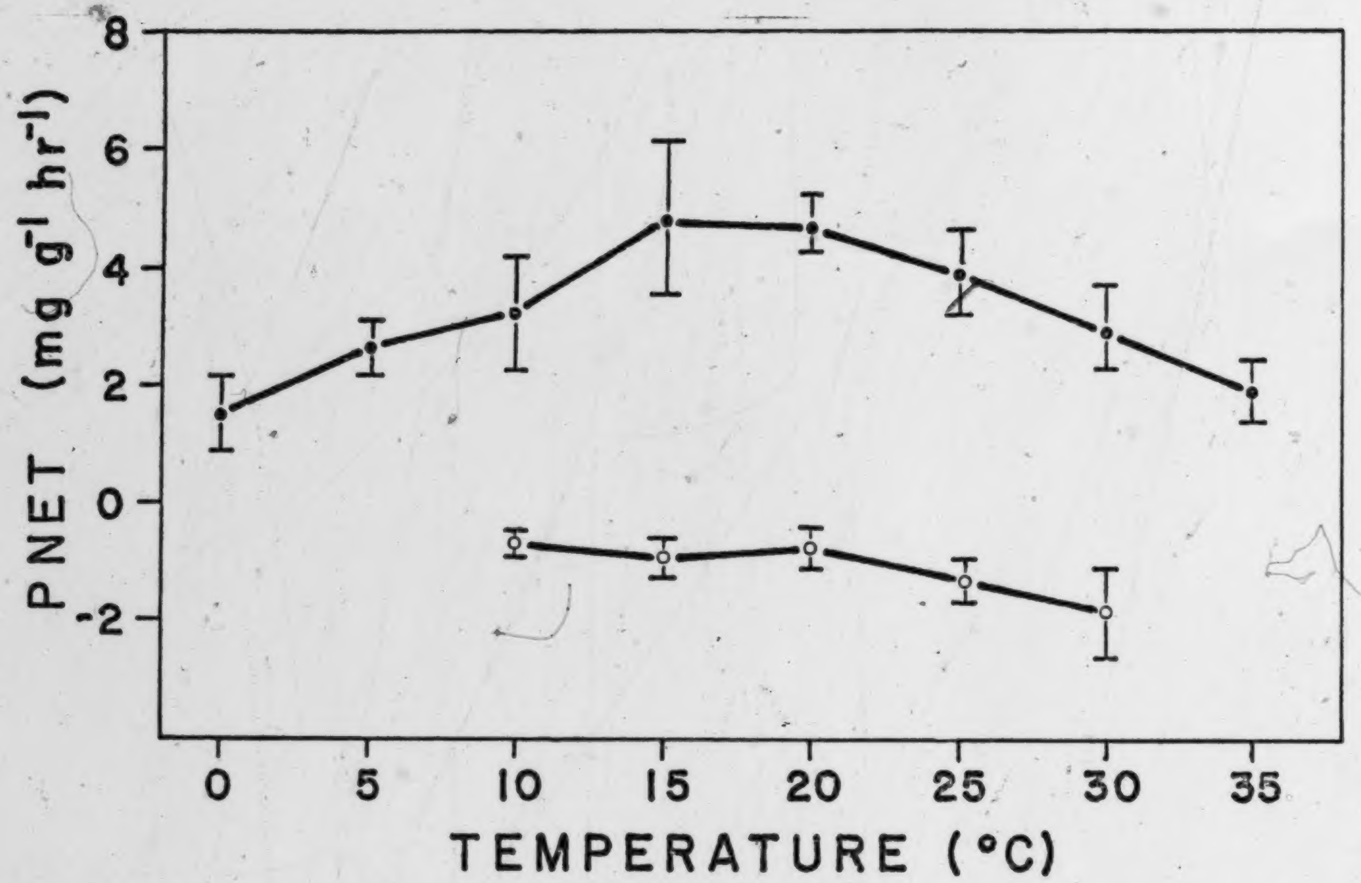

Figure 15. Temperature response of net photosynthesis for three year old seedlings (● =light response; ○ =dark respiration; bars are 95% confidence limits).

mg gm^{-1}hr^{-1} and 2 mg gm^{-1}hr^{-1} occurred at 0°C and 35°C respectively. Maximum dark respiration was 1.87 mg gm^{-1}hr^{-1} at 30°C with undetectable levels of respiration at 0°C and 5°C (Fig. 15).

Light response curves measured at 15°C show compensation for respiration occurred at 18 uEm^{-2}s^{-1} (Fig. 16). Saturation, when defined as the point at which a 100% increase in irradance resulted in less than a 10% increase in Pnet, occurred at 500 uEm^{-2}s^{-1}. Using the Michaelis-Menten model of enzyme kinetics (Lehninger 1970) applied to each of the 6 replicate curves the values for maximum Pnet (Vmax) and one-half maximum Pnet (1/2Vmax) were calculated. This required the addition of individual dark respirations to each measurement resulting in the interception of the origin as required by the model. The parameters for maximum Pnet and one-half Pnet were 5.91±1.18SD and 2.48±0.57SD respectively after subsequent removal of dark respiration. Temperature optima of 15°C compared well with published values (Vowinckel et al. 1975, van Zindern Bakker 1974) for *P. mariana*. Light response curves and light saturation points were similar to laboratory determined values by van Zindern Bakker but differ greatly from field observations by Vowinckel. Vowinckel reported much higher saturation light intensities of 1000 uEm^{-2}s^{-1}.

Photosynthetic measurements during the water stress

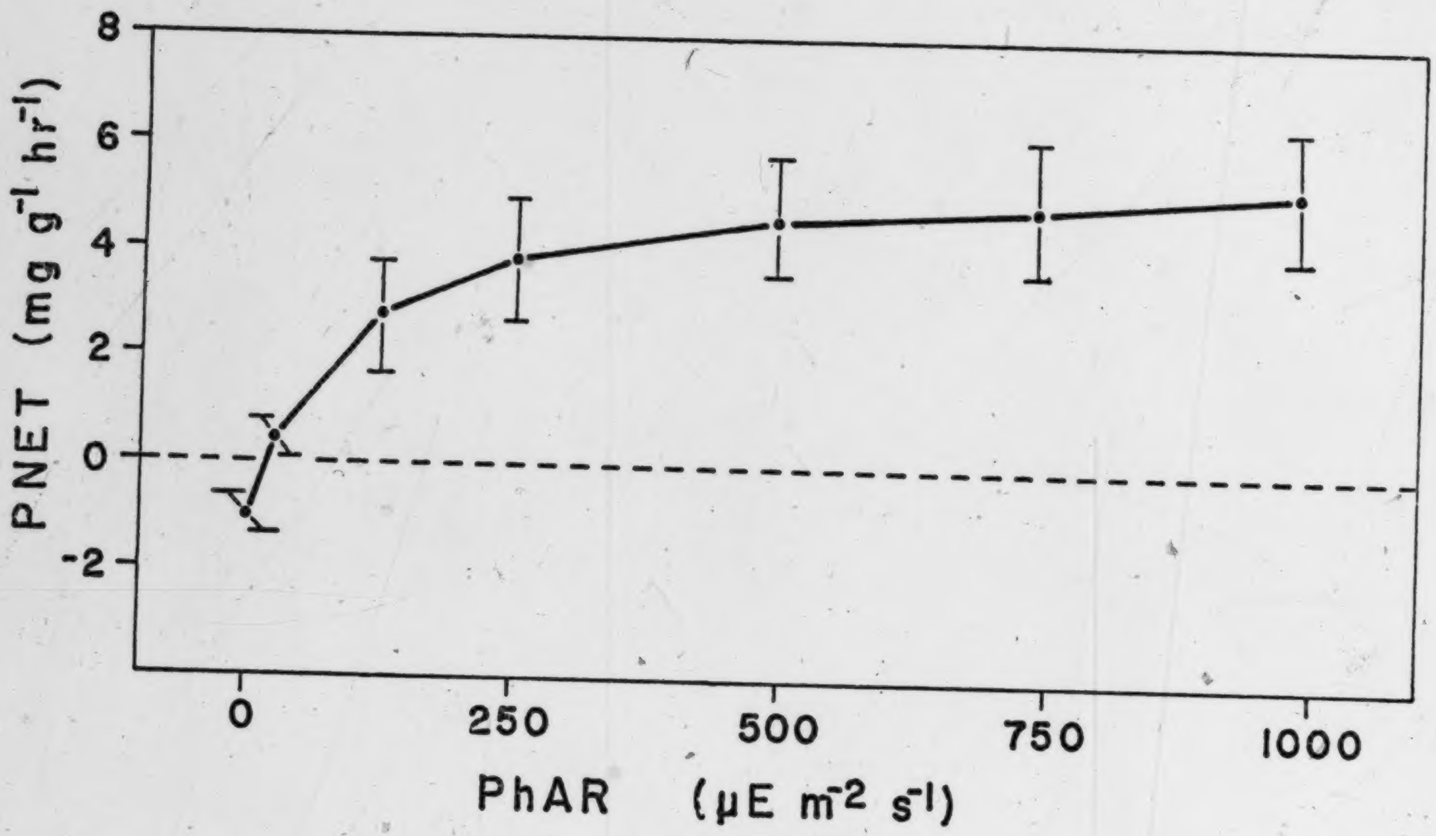

Figure 16. Net photosynthesis as a function of light intensity at 15°C for three year old seedlings. Bars are 95% confidence limits.

investigations were made at 15°C and 740 $uEm^{-2}s^{-1}$. Pnet of the same two seedlings were monitored while determinations of water content, water potential, combined osmotic and matric potentials and turgor potential were made on three "neighboring" seedlings. Measurements were made at the initiation of the drying run, the last watering and daily thereafter until day 5, whenafter morning and evening readings were made. Day 5 readings of -15 bar leaf water potentials resulted in a 50% reduction of Pnet and day 8 readings of -25 bar leaf potentials resulted in further reduction of Pnet to 0 (Fig. 17). Plots of turgor potential and combined osmotic and matric potentials (Fig. 18) showed no osmoregulation of turgor potential as found in field measurements and a lower correlation (r=0.5956 n=41) compared to field data (r=0.6564 n=42) for the relationship of water content to leaf potential (Fig. 19). Leaf water potential after watering of stressed plants recovered within 10 hr, but Pnet remained at 25% of original measurements; 100% recovery of Pnet was observed after 6 days.

C) Discussion

Seasonal trends in the water relations of *P. mariana* near Inuvik were found to be similar to those of *P. mariana* and *P. engelmannii* in other studies (Lindsay 1971,

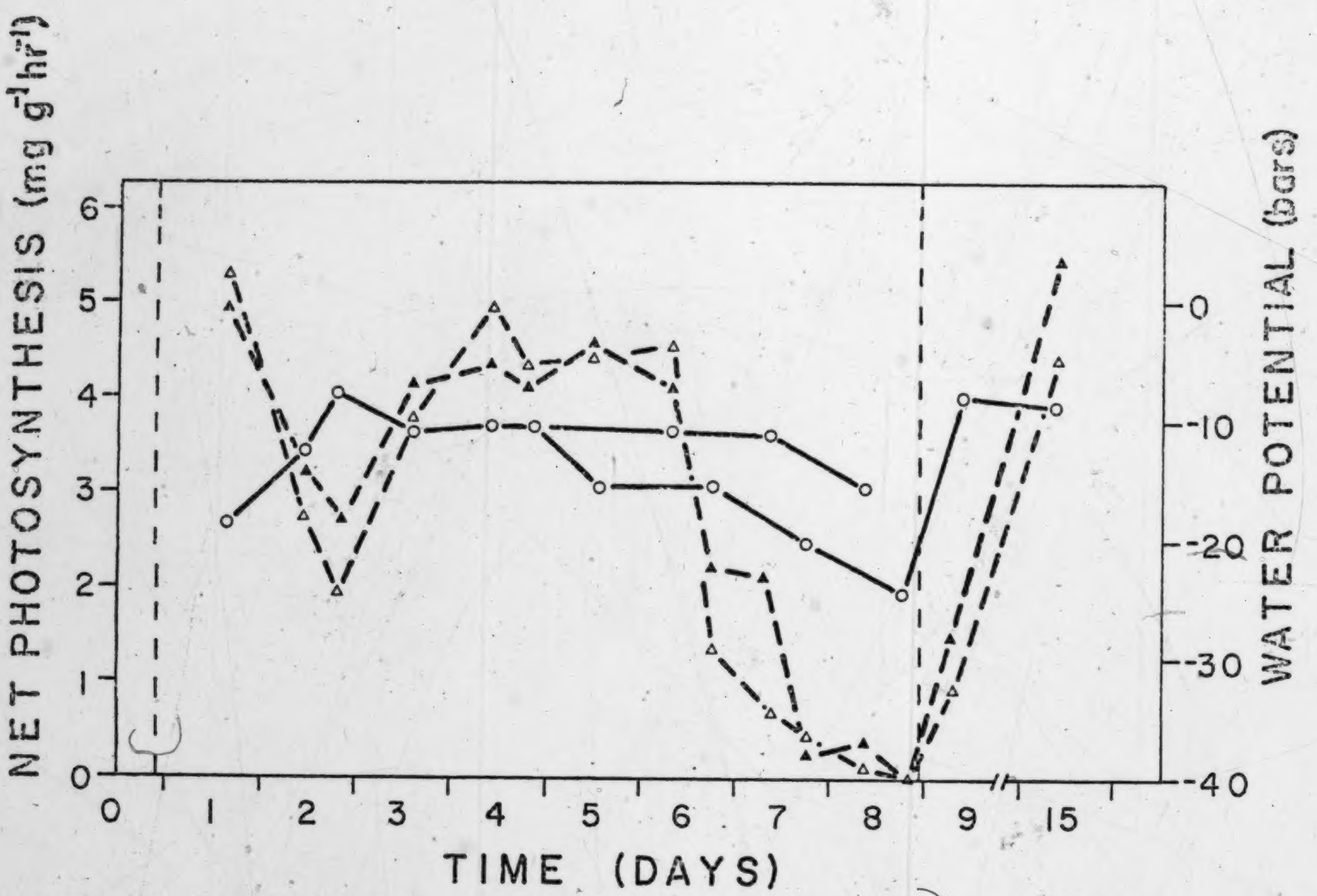

Figure 17. Net photosynthesis and water potential as a function of time since watering (▲=Pnet of seedling No.1; △=Pnet of seedling No.2; ○=Associated total leaf water potentials) split to morning and evening readings. Measurements were on three year old Picea mariana seedlings.

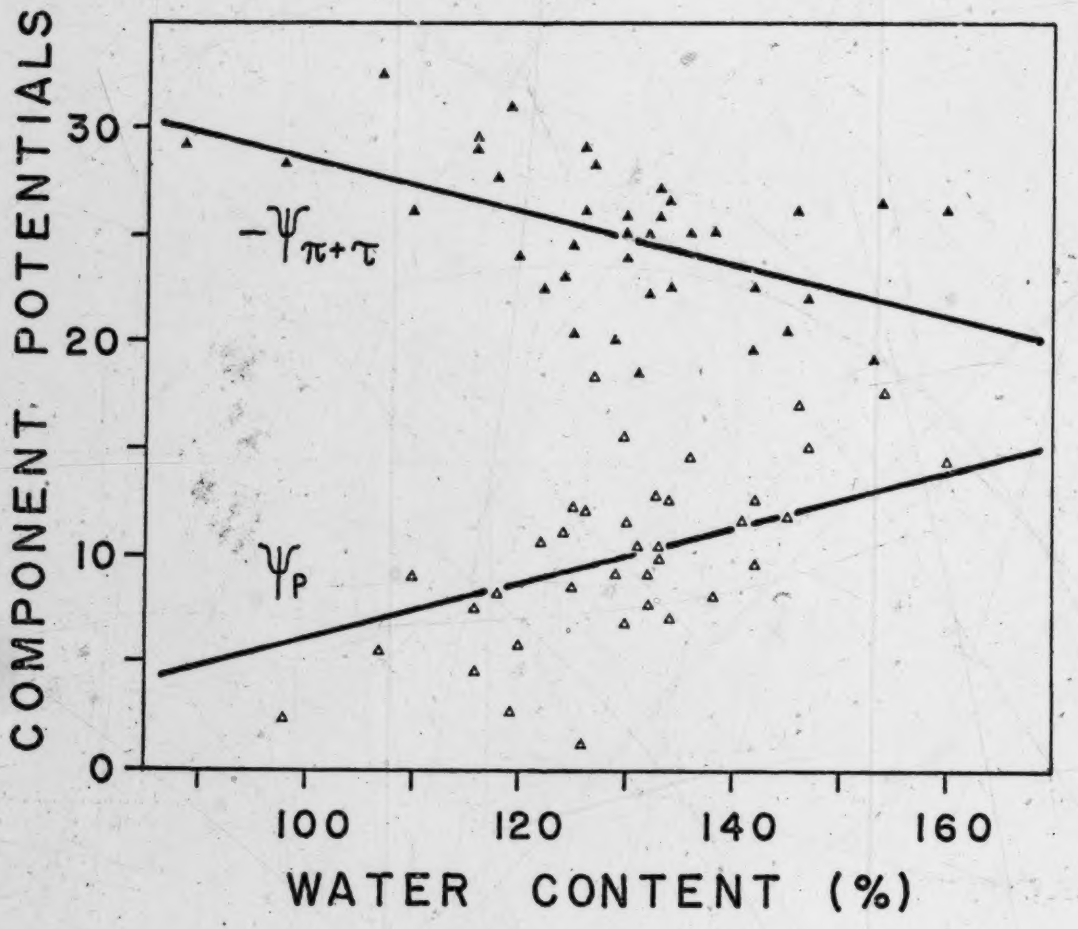

Figure 18. Laboratory determined osmotic and matric potentials and turgor potential as a function of water content for three year old *Picea mariana* seedlings (△ =turgor potential; ▲ =combined osmotic and matric potentials).

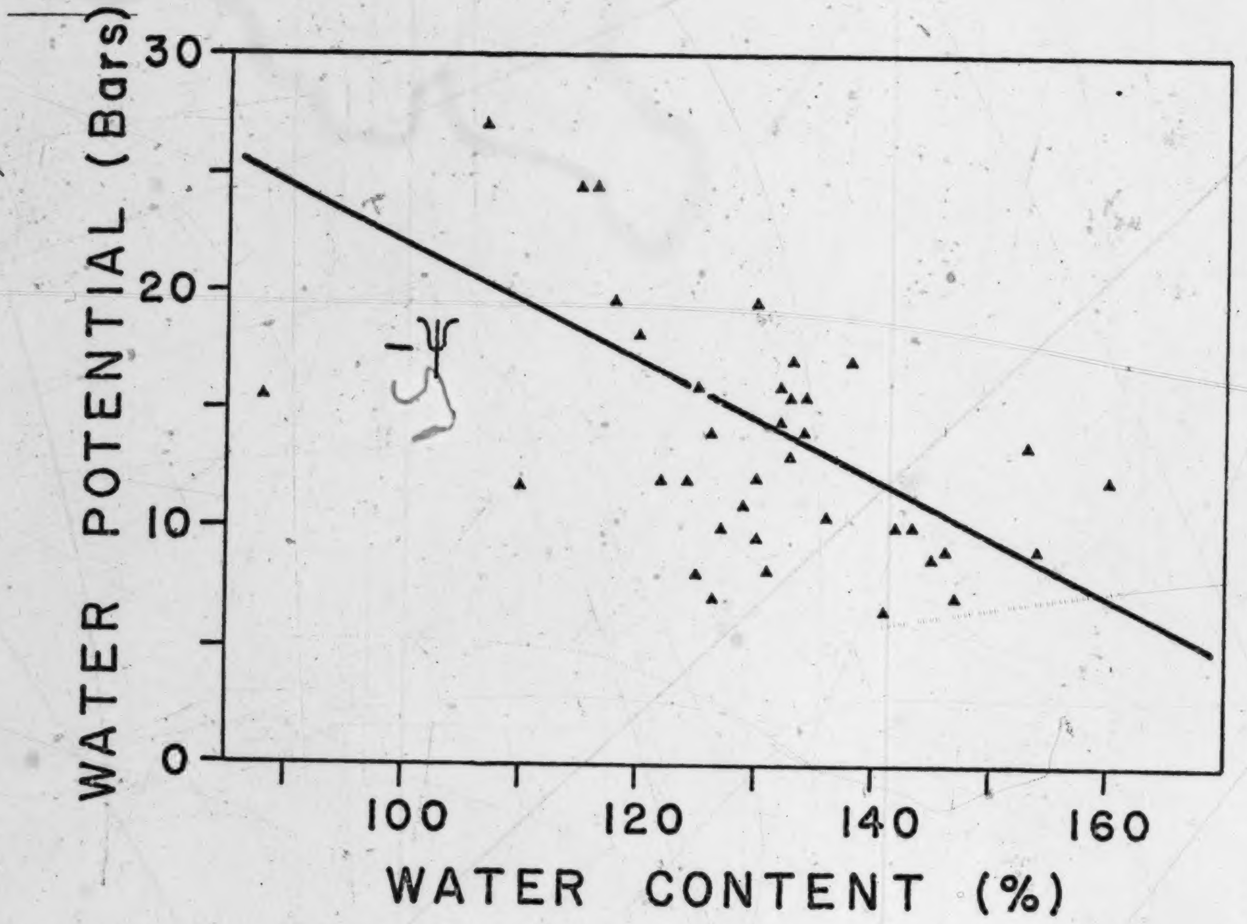

Figure 19. Total leaf potential as a function of water content for three year old *Picea mariana* seedlings.

Marchand 1975, van Zindern Bakker 1974). The high winter water content and leaf water potentials agree with Marchand's observation of _P. mariana_ on Mt. Washington, New Hampshire. This leads to the conclusion that winter water relations of trees near treeline are not important factors in determining distribution of _P. mariana_.

Low leaf water potentials during spring or early summer were also found by van Zindern Bakker (1974), who believed that maximum stress occurred with cold soils and high air temperatures. The unusually low values of the suppressed tree at Inuvik were not surprising in view of the relationship between tree density and water stress found in other conifers (Wambolt 1971).

The Pnet of _P. mariana_ showed sensitivity to water stress when compared to _Juniperus virginiana_, a drought tolerant successional species (Bacone et al. 1976). A 50% reduction occurred only after xylem tensions of -25 bars were attained (generally considered in close correlation to leaf water potential); a 90% reduction in Pnet resulted from -35 bar xylem tensions. Recovery rates of _Juniperus_ also reflected the drought ~~hardy~~ nature of the species with 85% recovery in 28 hr.

Water stress probably did not result in major inhibition of Pnet during 1976. Leaf potentials of -15 to -20 bar were only measured in the suppressed individuals and no apparent loss of turgor or stress-related needle cast was observed. It is therefore concluded that water stress or water stress related Pnet reduction in mature trees was not important in determining success of the species during 1976. Trees in the forest-tundra (Region I) have a reduced needle longevity of approximately six years compared to a norm of approximately 11 years (Regions II, III and IV). A possible explanation for this phenomenon is water stress resulting from anatomically immature needles, a response to shortened growing seasons as observed in European conifers (Baig and Tranquillini 1976).

Germling water relations could be used to explain mortality observed in field trials. The extreme sensitivity to water loss was a controlling factor in the success of the species on a local scale. Sensitivity of germlings to water stress has been used to explain the distribution of Tsuga canadensis (Olson et al. 1959); but this study is the first comparison of the change in water relations from germling to mature tree and the consequences of this for the species.

IV. SEED GERMINATION

A) Temperature Response

1. Methods

All cones were stored at -3°C until germination testing. No cold treatment was required due to previous overwintering of all seed tested. Seeds were extracted by soaking the cone in hot tap water for 6 hr, drying at 80°C for 8 hr in a forced air oven and tumbling to knock the seed free. Extracted seeds were dewinged and counted into lots of 50 seed for testing. Seeds were placed on No. 2 filter paper disks, treated with a mercurial fungicide (Morsodren, Morton Chemicals Ltd.) and transfered to 5 cm disposable petri dishes. Petri dishes were watered daily or as needed with distilled water. Germination was defined as radical elongation. Germinated seed were removed at 1-2 day intervals. All experiments were terminated after three weeks and all germination testing was done without illumination.

Temperature requirements for germination were investigated using 2 tests of 4 replicates of 2-5 year-old seed collected in Region II during 1975 and 1976. Temperature gradients were provided by a germination bar similar to Barbour and Racine (1967) enclosed in a controlled environment chamber. Temperature was held constant within ±1°C with replicates at 5°, 10°, 15°, 17°, 20°, 22°, 25°, 28°, 30° and 35°C. Thermal contact betweeen the plates and bar was insured by a thin layer of vaseline.

Temperatures were continuously monitered during the first test by a Grant Miniature Temperature Recorder. Periodically temperatures across the germinating surface were monitored with a Wescor MJ55 microvoltmeter and copper-constantan thermocouples.

Statistical treatment consisted of an arcsine transformation of the percentage germination data and complete factorial one-way analysis of variance (Sokal and Rohlf 1969). Duncan's multiple range test was used to isolate non-significant ranges of mean germinations.

2. Results

Temperature had a significant effect on germination (Table 6) with optimum temperature for germination (41%) occurring at 20°C (Fig. 20). Germination occurred at reduced levels at 15°, 17°, 25° and 28°C (Table 6) and was inhibited at 5°, 10°, 15°, 30° and 35°C. Seed from lower temperature trials (5°, 10°, 15° and 17°C) germinated when placed in temperatures condusive to germination (20°C); while seed from higher temperature (30° and 35°C) did not respond to optimal temperatures. They were probably killed by the higher temperatures.

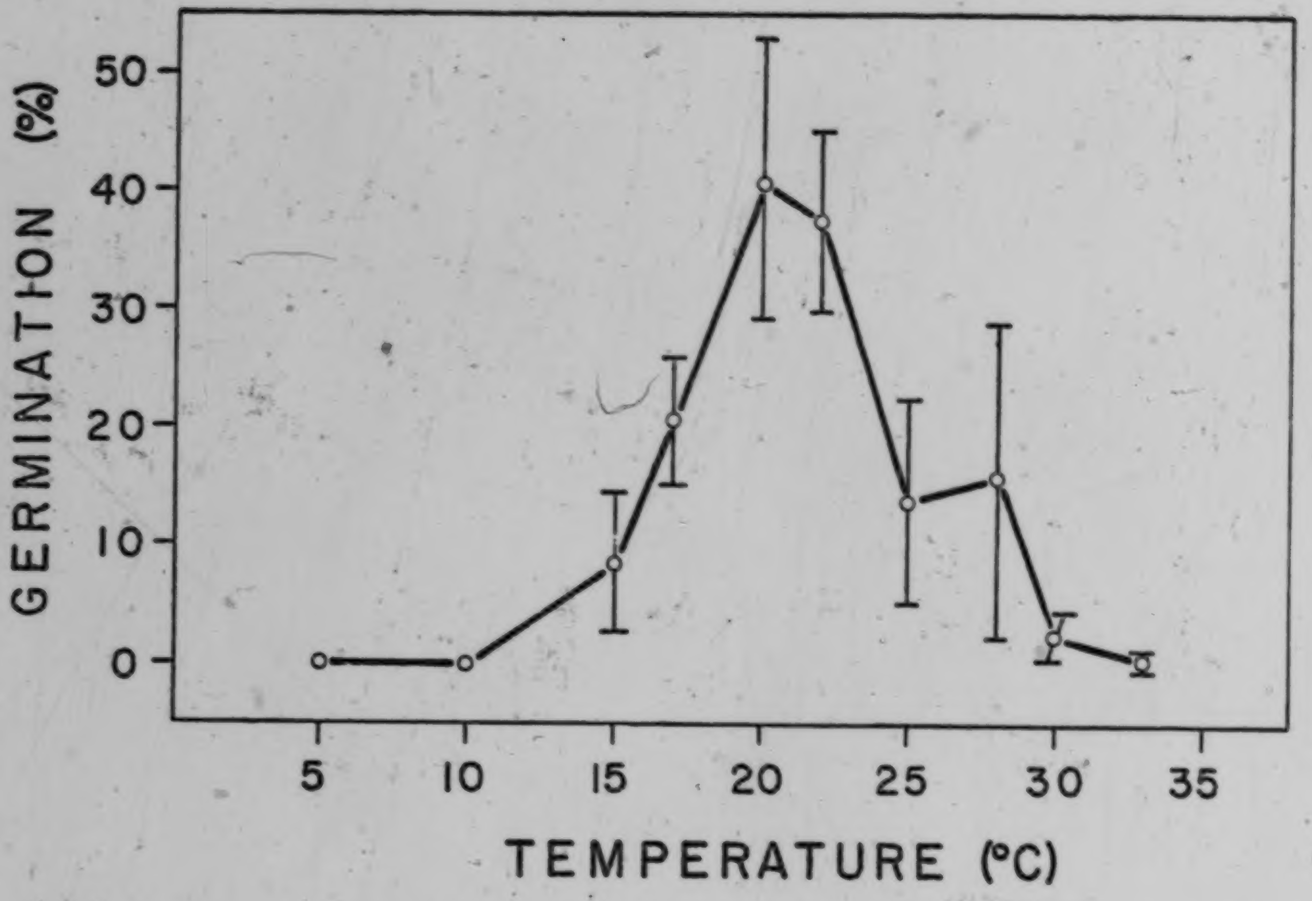

Figure 20. Germination as a function of temperature for *Picea mariana* seed. Vertical bars are 95% confidence limits.

Table 6. Analysis of variance and non-significant ranges for germination temperature relations *P. mariana* primarily from Regions II, III and IV.

Factor	DF	MS	F	Probability
Replicates	7	0.0147	0.91	non-sign
Treatment	9	0.5241	32.47	P<0.001
Error	63	0.01615		
Total	79			

Germination percents

Temperature	5°	10°	15°	17°	20°	22°	25°	28°	30°	35°
Germination	0	0	9	21	41	38	14	16	3	1
Non-significant Ranges					———	———				
				———	······	······	———	———		
	———	———	———	······	······	······	······	······	———	———

B) Regional Germination

1. Methods

Regional variation in seed germination was investigated using cone samples collected in each of the four designated forest regions. At the time of collection, cones were separated into 1, 2-5 and 5+ year-old samples. Storage, extraction, germination and statistical analysis were as described previously for temperature testing, except all tests were conducted at 20°C in a controlled environment chamber.

Regional differences in seed size were investigated using 4 replicates of 50 seeds 2-5 years in age. Seeds were weighed with wings intact; data are expressed in seeds per kilogram. Data analysis was similar to that for the germination trials.

2. Results

Germination was greatest (28-35%) in 2-5 year-old seed samples with non-significant differences between Regions II, III and IV (Tables 7 and 8). Most important, no germination was observed from Region I, the forest-tundra region. Seed size was not significantly different in the three forest regions, 0.97-1.32 X 10^6 seeds Kg^{-1}, but seed was less than one-half as large in the forest tundra region (2.28 X 10^6 seeds Kg^{-1}, Table 9).

Germination in the 5+ year-old seed was not significantly different in the 3 regions tested (Table 7). Region IV seed was inadvertently destroyed before testing. Seed 5+ years old gave the only germination (0.5%) from the forest-tundra indicating how rare successful seed set is in this region.

Seed samples (1 year-old) initiated in 1975 show a gradient of increasing germination from north to south of 0, 1.5, 4 and 7% for Regions I, II, III and IV, respectively, and a gradient of non-significance between them (Table 8).

Table 7. Analysis of variance for regional differences in germination of *P. mariana* seed of differing ages.

Factor	DF	MS	F	Probability
1 year-old seed				
Replicates	3	0.0117	1.52	non-sign
Treatment	3	0.0467	4.01	P<0.05
Error	9	0.0070		
Total	15			
2-5 year-old seed				
Replicates	3	0.0074	1.89	non-sign
Treatment	3	0.1098	28.22	P<0.001
Error	9	0.0039		
Total	15			
5+ year-old seed				
Replicates	3	0.0132	1.54	non-sign
Treatment	2	0.0187	2.19	non-sign
Error	6	0.0086		
Total	11			

Table 8. Non-significant ranges for regional percent germination of *P. mariana* (P=0.05).

Region	I	II	III	IV
1 year-old seed Percent Germination	0	1.5	4	7
Non-significant Ranges			————	————
		————	————	
	————	————		
2-5 year-old seed Percent Germination	0	34	28	35.5
Non-significant Ranges		————	————	————
5+ year-old seed Percent Germination	0.5	3	3.5	

Table 9. Analysis of variance and non-significant ranges of regional seed sizes (P=0.05).

Factor	DF	MS	F	Probability
Replicates	3	0.1373	3.80	non-sign
Treatement	3	1.4068	38.00	P<0.001
Error	9	0.361		
Total	15			

Seed sizes

Region	I	II	III	IV
Seed$X10^{6}$ Kg^{-1}	2.28	1.08	0.97	1.32
Non-significant Ranges		————	————	
		————	··············	————

C) Discussion

Temperature appears to be of primary importance in controlling germination of P. mariana even in these northern populations. The importance of the 15°C lower cardinal temperature for germination will be discussed further in relation to field germination trials but it should be noted that the same 15°C temperature limitation was found in populations of P. mariana from the southern Northwest Territories to Michigan (Fraser 1970). This inhibition was not reported to be reversible by Fraser. The inhibition and probable death of seed above 28°C was less well defined when compared to Fraser's work but may be instrumental in elimination of germination for buried seed populations of

P. mariana (Fraser 1976, Johnson 1975).

Environmental effects on germination would best be seen where the unusually cool summer of 1974 (Fig. 4) resulted in reduced germination of the 1975 produced seed in a north to south gradient. A one year delay in environmental effects on cone initiation in *P. mariana* was previously observed in Ontario by Fraser (1966) and it is probable that such environmental effects extend to germination as well. Environmental effects on seed development may help explain the reduced germination of 35% in this study from the reported values of 40-60% (Vincent 1965, Zazada 1971). Seed size may elucidate this problem of reduced germination as reported seed weights of 0.89 X 10^{6} seeds Kg^{-1} (Vincent 1965) were greater than values in this study, especially for seed from the forest-tundra region. Reduced seed size may also explain the reduced longevity observed (3% germination at 5 years in the Inuvik population) for Chai and Hansen (1952) reported germinations of 32% at 5 years, 8% at 10 years and 1% at 15 years.

Environmental effects on reproduction therefore probably act on the initial magnitude of and longevity for germination, before the seed mature. The environment also has the important potential of interfering with germination of the seed through the lower cardinal temperature.

V. GERMLING RESPONSE TO ENVIRONMENT

1. Methods

Microsites within soil hummock topography were chosen in 1975 and 1976 representing the microenvironment encountered by germling *P. mariana* in a post-fire subarctic woodland. These were characterized as hummock top, side and trough microsites by the following criteria: 1.) Hummock top microsites were the exposed (after fire) mineral soil core of a discrete soil hummock. Little or no vegetation and no organic material covered the mineral soil. 2.) Hummock side microsites were adjacent to the previous microsite but were microtopographically lower with an organic covering of increasing thickness away from the hummock top. These contained a vegetative covering of *Polytrichum commune*, *P. juniperinum*, *Marchantia polymorpha*, *Ceratodon purpureus* and *Bryum psuedotriquetrum* along with other cryptogamic species. 3.) Hummock trough microsites were the lowest and were characterized by a peat soil and water table at the soil surface in early June. Vegetative cover was similar to the hummock side microsite but with more luxuriant growth of *Polytrichum*.

No aspect related pattern was found in the pre-burn distribution of *P. mariana* trees but nevertheless microsites were chosen minimizing bias with respect to aspect. Living moss and peat were removed down to the charred post-fire surface in an area twice the size of the 4 dm^2 square plots, and all vascular plants were clipped from the plots but were subsequently permitted to regrow.

Seeds collected in Region II were extracted, dewinged, counted into 250 seed lots and stored at -3°C. No chemical fungicides or predation deterrents were used. Randomly chosen seed sub-samples were tested for germination of the 1976 sample (33.6% ±5.5SD) and assumed similar for the 1975 sample. 1975 samples were falsely tested as outlined by U.S.D.A (1948) and were discarded.

Seed (250 seed $plot^{-1}$) were hand sown into plots within three weeks after snow release in 1975 (14 June, Site N and 12 June, Site S) and within two weeks in 1976 (5 June, Site N and 4 June, Site S). Care was taken to distribute seed evenly within each of six replicate plots for each microsite (top, side and trough). Adjacent each replicate plot was permanently marked with 1.2X100 cm metal stakes and plot corners marked with small nails for easy relocation.

Permanent records of recruitment and mortality for test germlings were made with a mapping table (Fig. 21) afixed to the permanent markers. Care was taken to level the table, thus producing an accurate map of germling positions. Plots were checked at six day intervals and on 28 September 1975. Background rain of seed did not occur and all germlings were assumed to originate from the test seed lots.

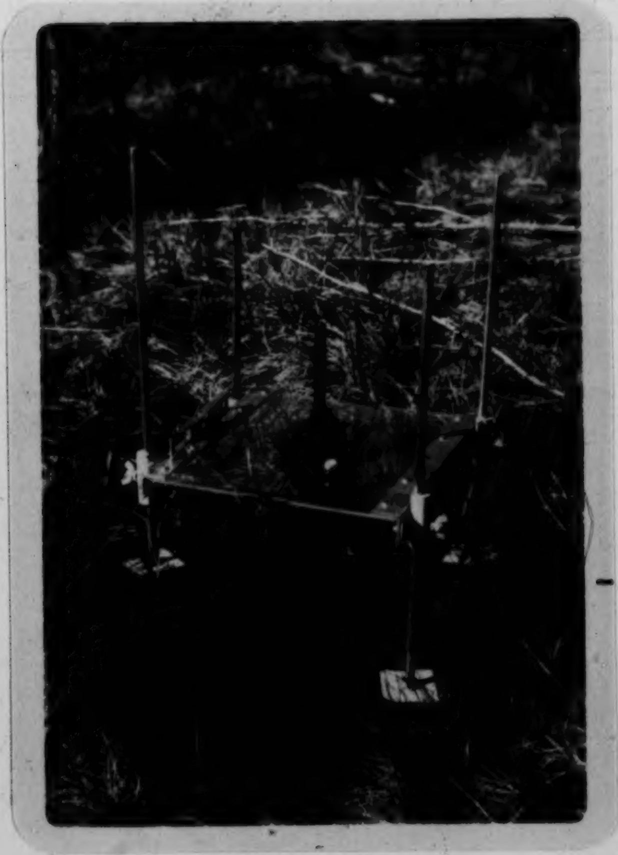

Figure 21. Mapping table used for germination and survivorship study, set over an experimental plot. The black object is the sighting tube.

Germination was expressed as percent of the 250 seed which germinated and mortality as percent of total germinations by plot. Data analysis consisted of an arcsine transformation of percentage germination and mortality data and three-way complete factorial analysis of variance using regional site, microsite and time as the treatments. Non-significant ranges of germination and mortality were determined by Duncan's multiple range test using error mean squares generated from one-way analysis of variance for individual microsites. Comparison of means tests were used to test significant differences between summations of germination, mortality and subgroups of mortality.

Environmental measurements were made as described in the site descriptions and qualitative assessment of the hummock microenvironment was made with ten replicate transplants of 5-7 year-old seedlings into each microsite.

2. Results

Germination

Regional site, microsite and time interacted in 1975 producing a significant component of variance (Table 10), but only interactions of regional site with time and microsite with time were significant in 1976 (Table 11). Non-significant differences between all germinating sites (Table 12) in 1976 resulted in the change in interaction

Table 10. Complete factorial analysis of variance for field germination trials of *P. mariana* in 1975.

Factor	DF	MS	F	Probability
Replicates	5	0.00063	0.86	Non-sign
Interaction				
SiteXmsiteXtime*	24	0.00310	4.21	P<0.001
Error	385	0.00074		
Total	467			

* msite=microsite

Table 11. Complete factorial analysis of variance for field germination trials of *P. mariana* in 1976.

Factor	DF	MS	F	Probability
Replicates	5	0.000199	0.46	Non-sign
Interaction				
SiteXmsiteXtime	16	0.000437	0.98	Non-sign
TimeXmsite	16	0.001419	3.25	P<0.001
TimeXsite	8	0.000986	2.26	P<0.025
SiteXmsite	2	0.000551	1.26	Non-sign
Error	265	0.000437		
Total	323			

variances.

Microtopographic effects on germination were similar in 1975 and 1976 with germination restricted to hummock sides and troughs. Seed failed to germinate in 1975 and 1976 on hummock top microsites. Otherwise substrates were not directly responsible for variance in germination between microsites as differences were not significant between total germination at the same regional site (Table 13).

Table 12. Field germination summaries for *P. mariana* in 1975. *

ANOVA for germination of all germinating sites

Factor	DF	MS	F	Probability
Replicate	5	0.00183	0.63	non-sign
Treatment	3	0.02811	9.66	P<0.001
Error	15	0.00291		
Total	23			

Total field germinations for 1975

	Site N		Site S	
	Side	Trough	Side	Trough
Percent germination	3.5	3.9	9.1	10.1
Non-significant ranges	————	————	————	————

* Hummock top values (0%) were not used in the analysis.

Table 13. Field germination summaries for *P. mariana* in 1976. *

ANOVA for germination of all germinating sites

Factor	DF	MS	F	Probability
Replicates	5	0.0008	0.24	non-sign
Treatment	3	0.0055	1.62	non-sign
Error	15	0.0034		
Total	23			

Percent germination for all microsites

	Site N		Site S	
	Side	Trough	Side	Trough
Percent germination	1.2	1.1	1.0	0.4

Grand mean 0.92%

* Hummock top values (0%) were not used in the analysis.

Together, regional and microsite temperatures control the initiation of germination. All germination occurred after three day mean (+5 cm) temperatures were greater than 15°C (Figures 22-33). Temperatures at +5 cm were found more highly correlated (r=0.7659, n=70) with soil surface temperatures than were -3 cm (r=0.6801, n=70). Air data were used in all comparisons.

Germination peaks occurred before 8 July in 1975 for the hummock side microsite at both regional sites (Figs. 23 and 26). Germination peaks for the trough microsites were delayed compared to side microsites, reflecting a difference in air (0.5°C) and soil (4-5°C) temperatures. Germination was not significant after mid July (Tables 14, 15, and 16) even with temperatures in the optimal ranges, due to low soil water. Significant germination peaks in 1976 were delayed until the second week in July or did not occur (trough microsite, Site S) due to low spring temperatures (Figs. 28-33). No significant germination occurred after the fourth week of July 1976 (Tables 17, 18 and 19).

Temperature differences between regional sites and yearly trials provide the best predictive insight for germination of P. mariana. The regional mean temperature for June 1975 and 1976 was significantly correlated ($P<0.05$) with microsite germination (Fig. 34, pg. 78) corroborating the temperature limitation to germination found in laboratory trials. July mean macrosite temperatures were not

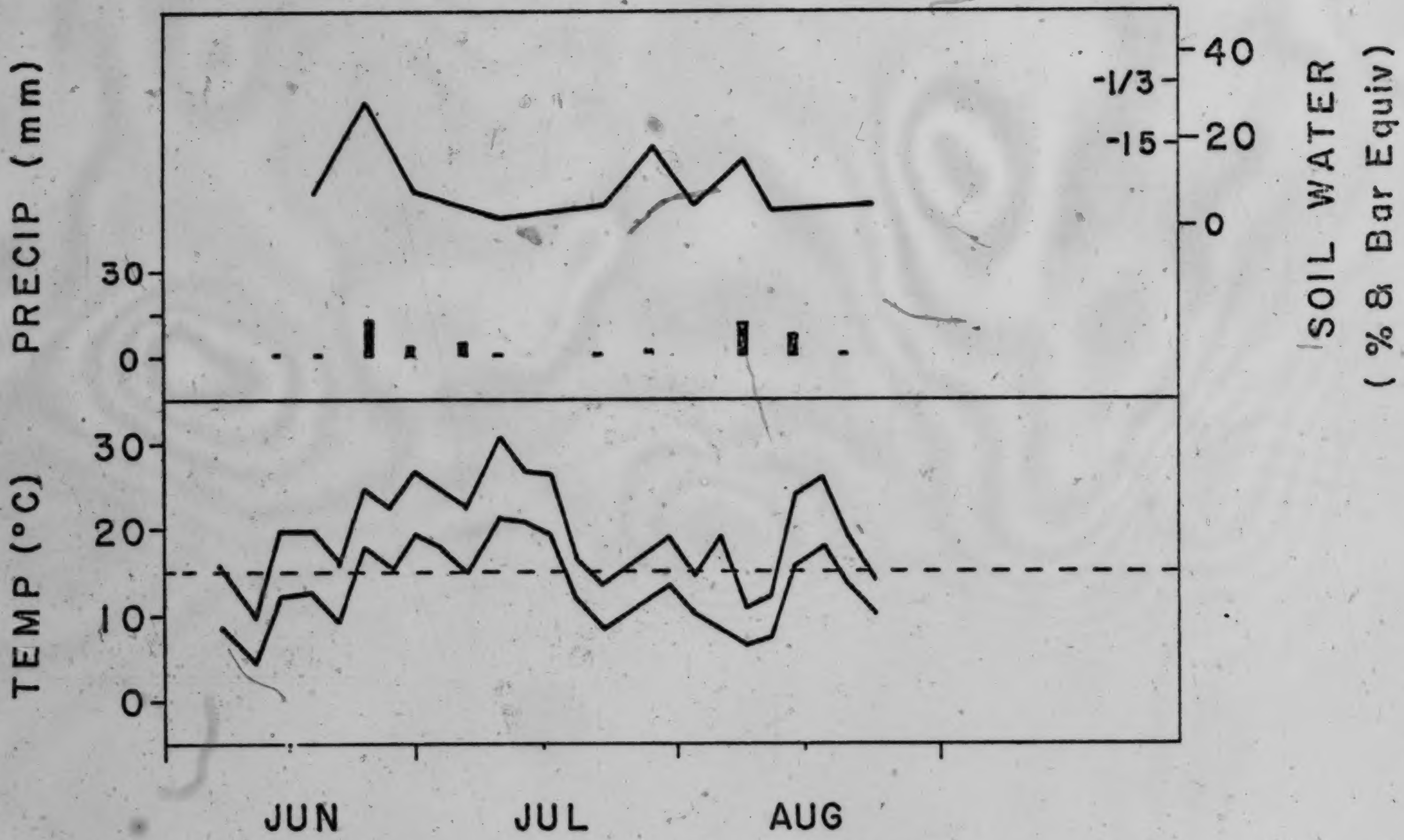

Figure 22. Environmental data from Site N hummock top microsite for 1975. In the top graph the line is soil water content and bars are six day sums of precipitation. In the lower graph the lines are three day means of maximum temperature (upper) and daily mean temperature (lower).

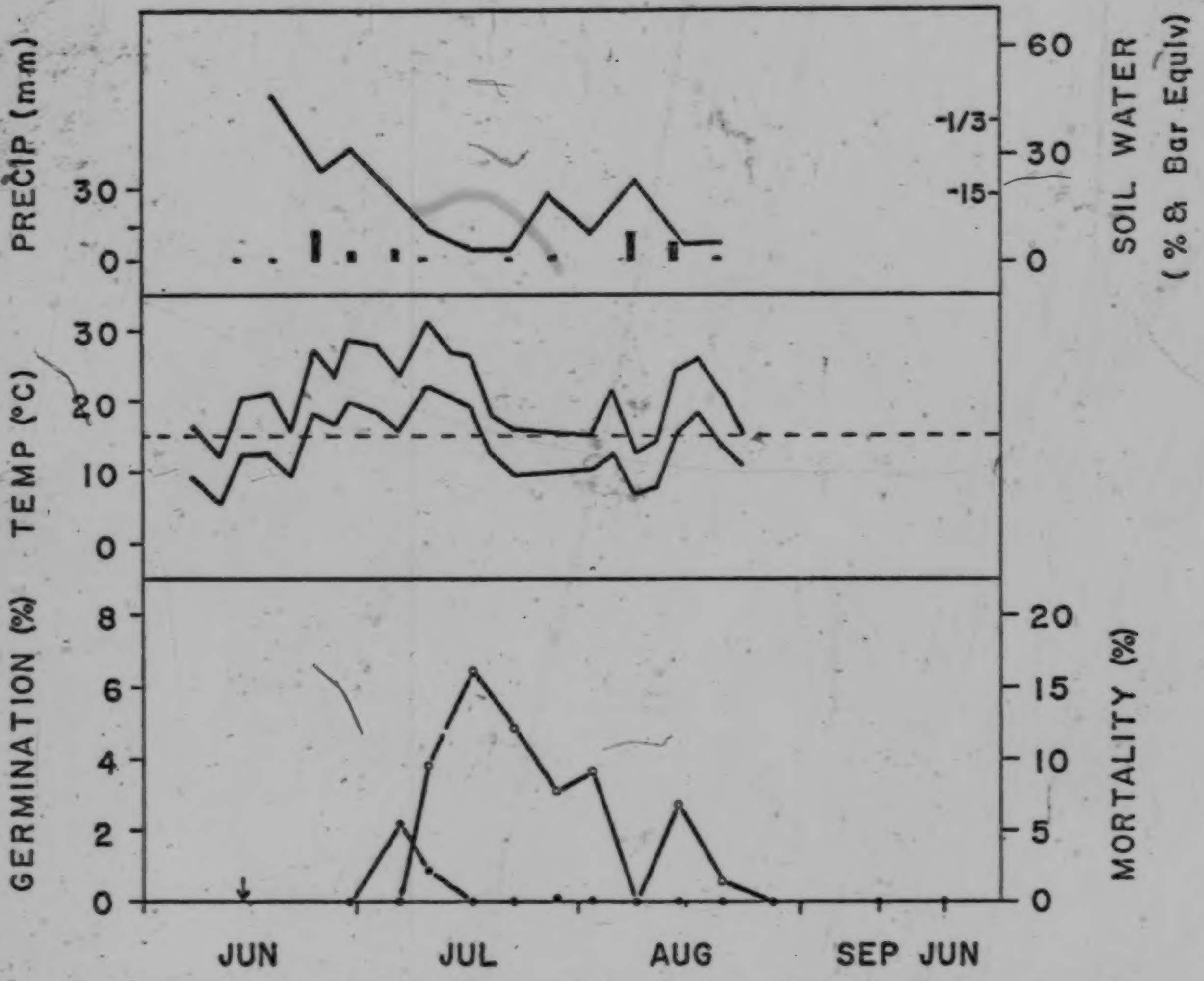

Figure 23. Enviromnental, germination and mortality data from Site N hummock side microsite for 1975. In the top graph the line is soil water content and bars are six day sums of precipitation. In the middle graph the lines are three day means of maxmum temperature (upper) and mean daily temperature (lower). The lower graph is germination (●), germling mortality (○) and date of sowing (↓).

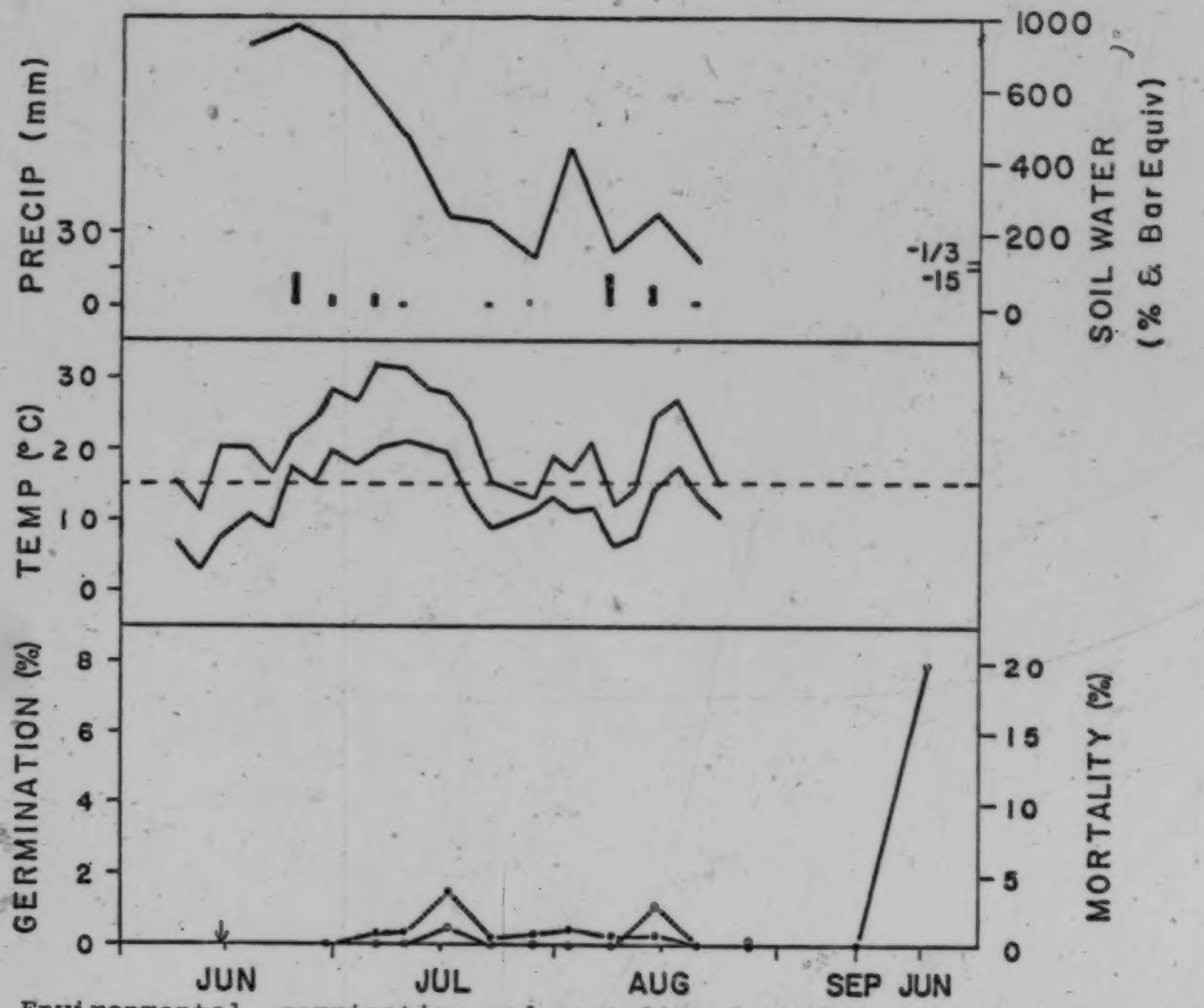

Figure 24. Environmental, germination and mortality data from Site N hummock trough microsite for 1975. In the top graph the line is soil water content and bars are six day sums of precipitation. In the middle graph the lines are three day means of maximum temperature (upper) and mean daily temperature (lower). The lower graph is germination (●), germling mortality (o) and date of sowing (↓).

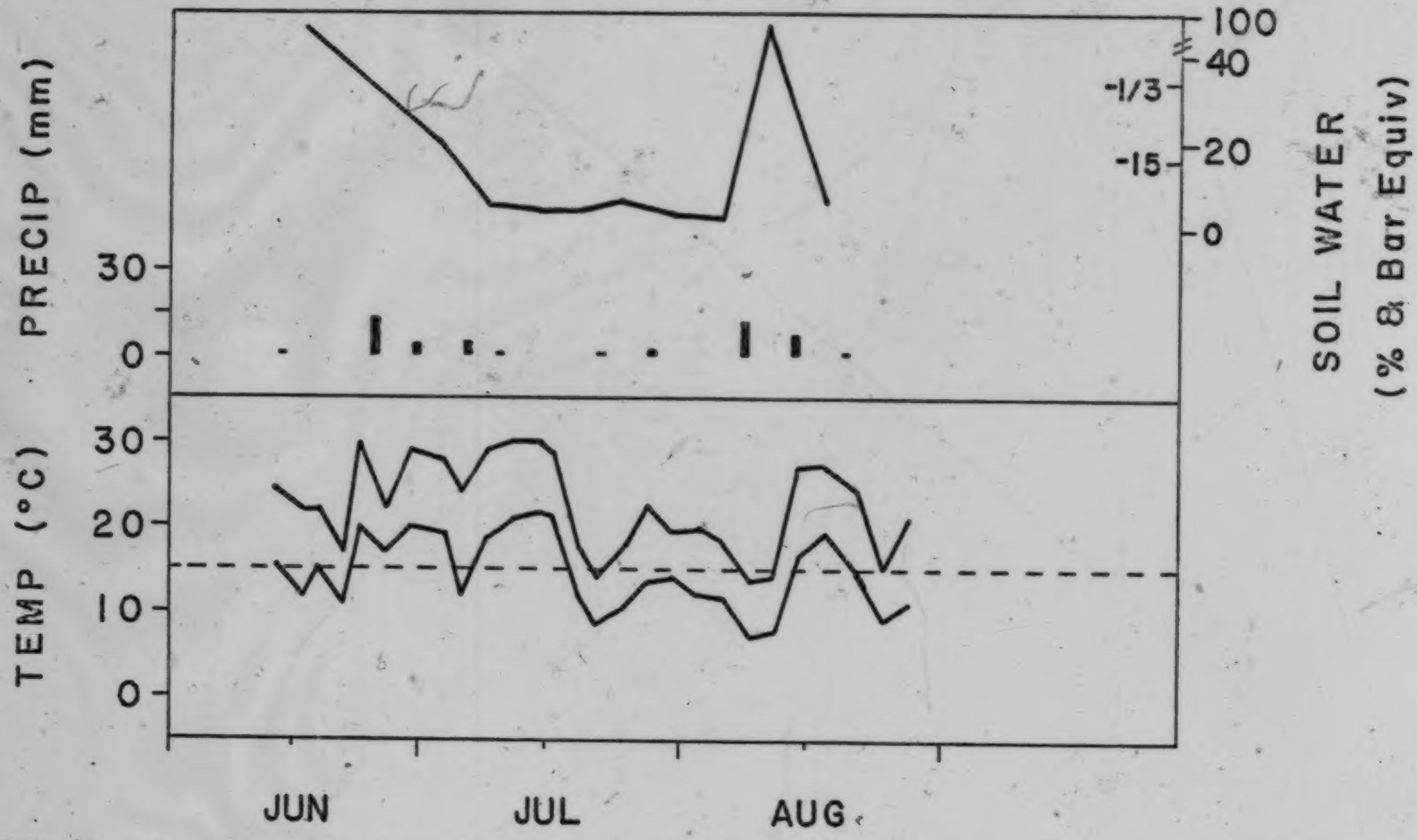

Figure 25. Environmental data from Site S hummock top microsite for 1975. In the top graph the line is soil water content and bars are six day sums of precipitation. In the lower graph the lines are three day means of maximum temperature (upper) and daily mean temperature (lower).

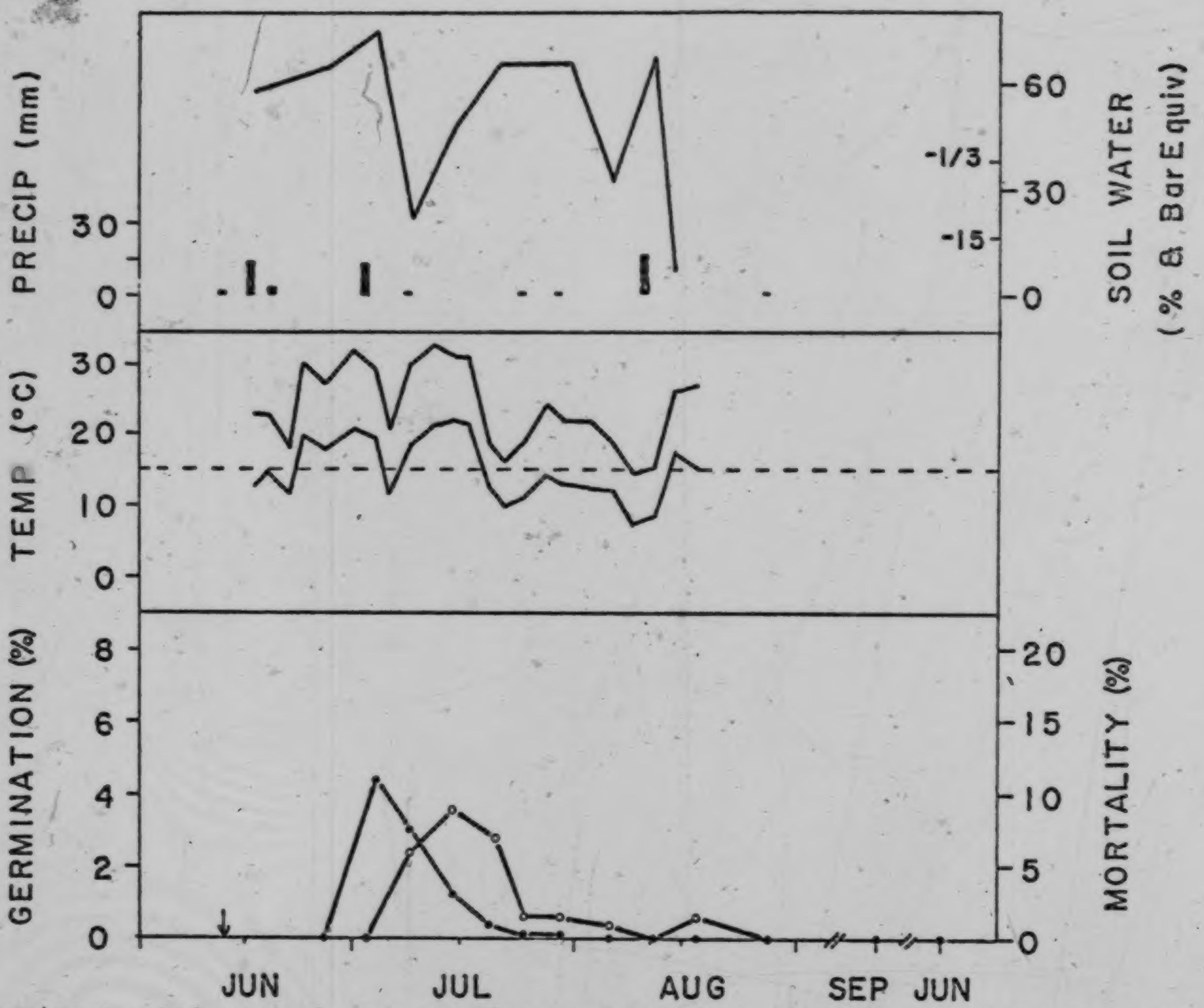

Figure 26. Environmental, germination and mortality data from Site S hummock side microsite for 1975. In the top graph the line is soil water content and bars are six day sums of precipitation. In the middle graph the lines are three day means of maximum temperature (upper) and mean daily temperature (lower). The lower graph is germination (●), germling mortality (○) and date of sowing (↓).

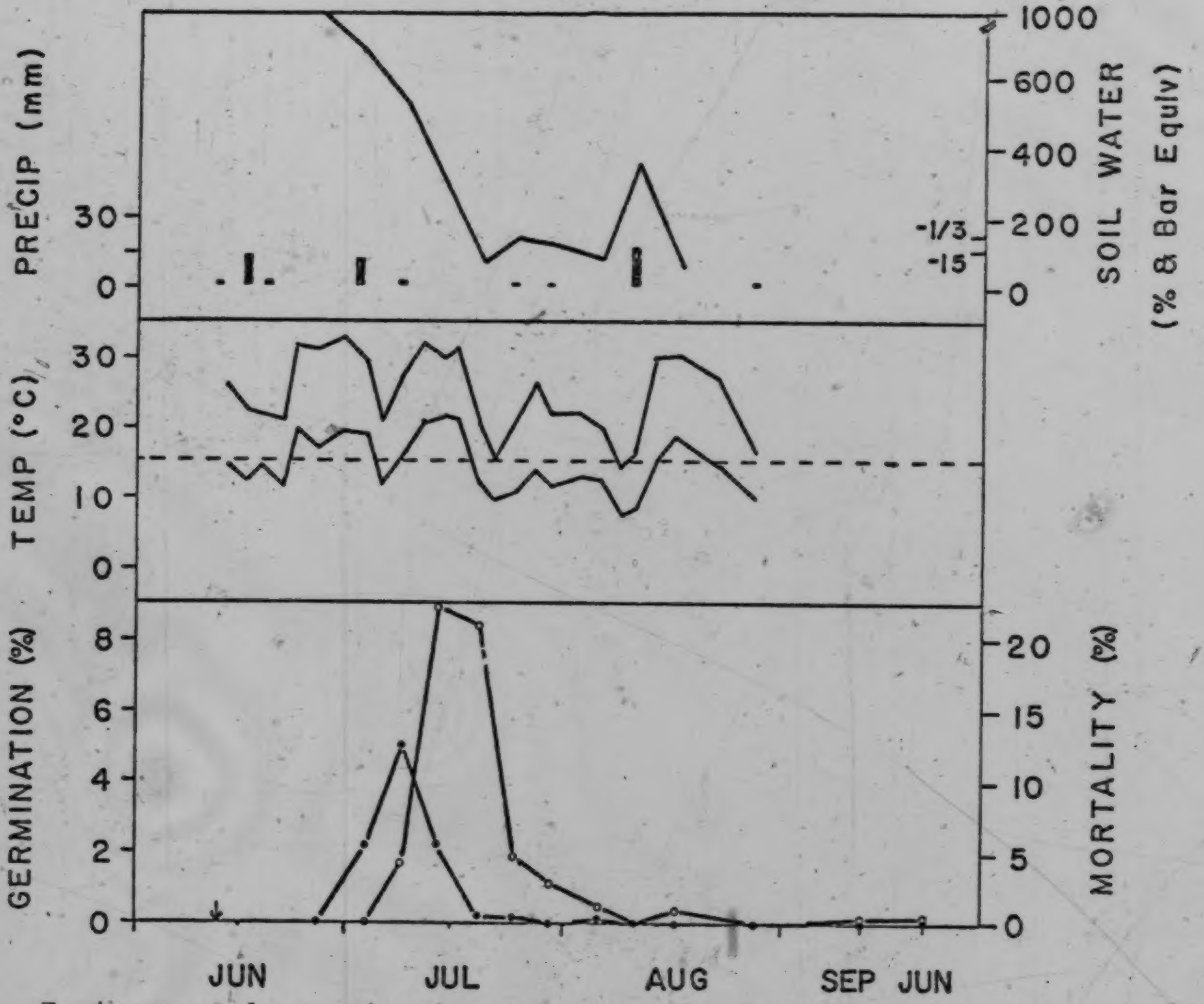

Figure 27. Environmental, germination and mortality data from Site S hummock trough microsite for 1975. In the top graph the line is soil water content and bars are six day sums of precipitation. In the middle graph the lines are three day means of maximum temperature (upper) and mean daily temperature (lower). The lower graph is germination (●), germling mortality (○) and date of sowing (↓).

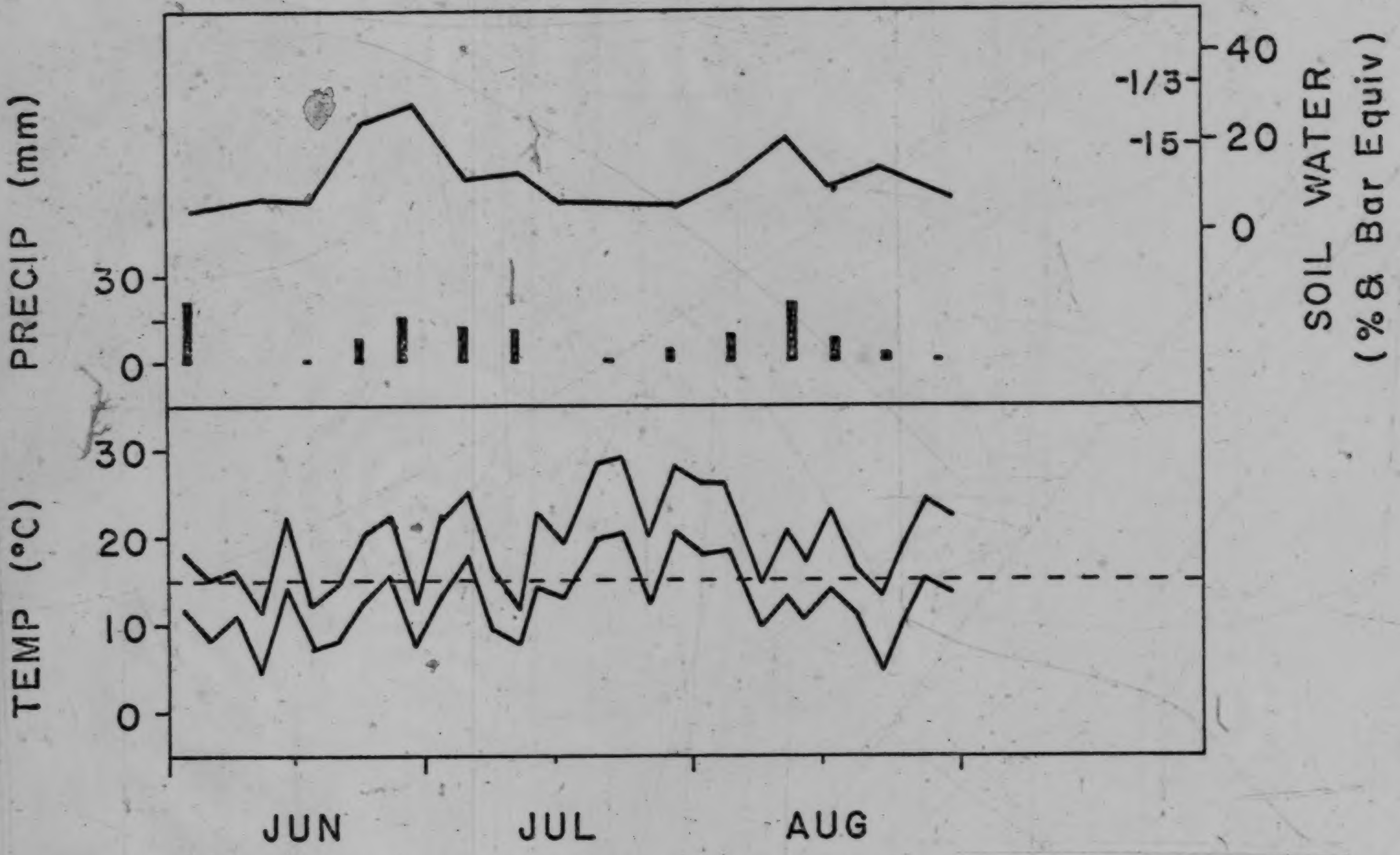

Figure 28. Environmental data from Site N hummock top microsite for 1976. In the top graph the line is soil water content and bars are six day sums of precipitation. In the lower graph the lines are three day means of maximum temperature (upper) and daily mean temperature (lower).

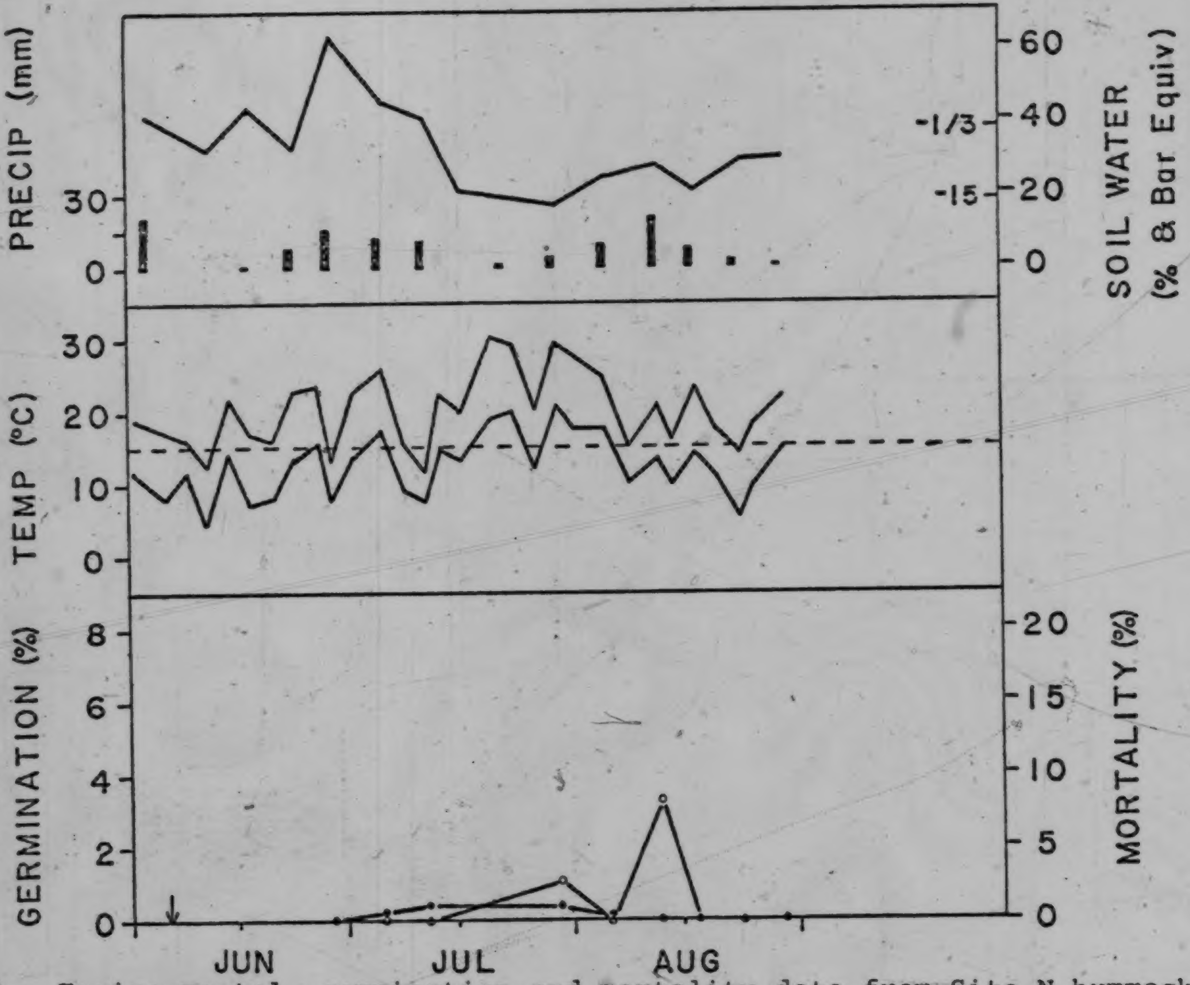

Figure 29. Environmental, germination and mortality data from Site N hummock side microsite for 1976. In the top graph the line is soil water content and bars are six day sums of precipitation. In the middle graph the lines are three day means of maximum temperature (upper) and mean daily temperature (lower). The lower graph is germination (●), germling mortality (o) and date of sowing (↓).

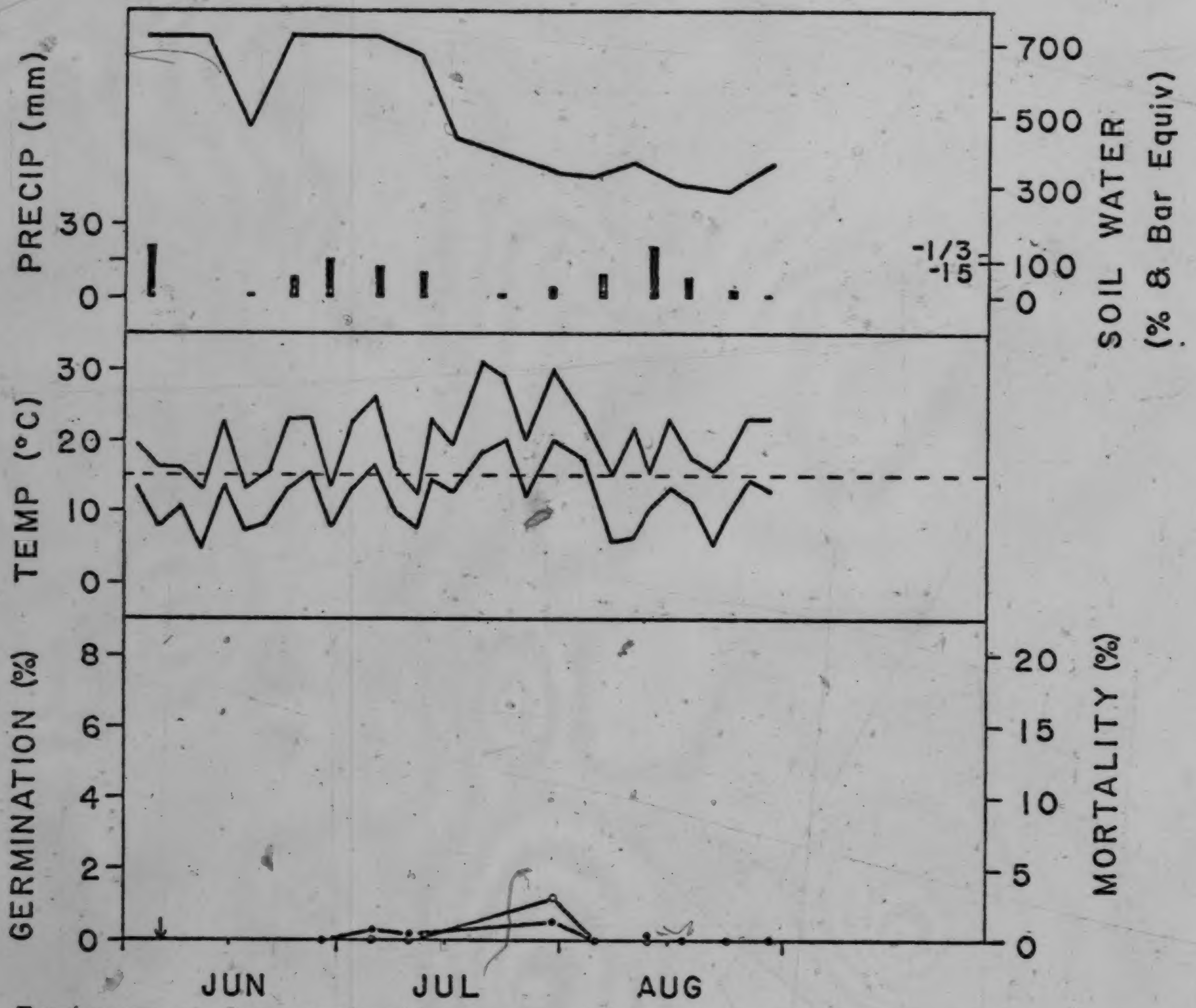

Figure 30. Environmental, germination and mortality data from Site N hummock trough microsite for 1976. In the top graph the line is soil water content and bars are six day sums of precipitation. In the middle graph the lines are three day means of maximum temperature (upper) and mean daily temperature (lower). The lower graph is germination (●), germling mortality (○) and date of sowing (↓).

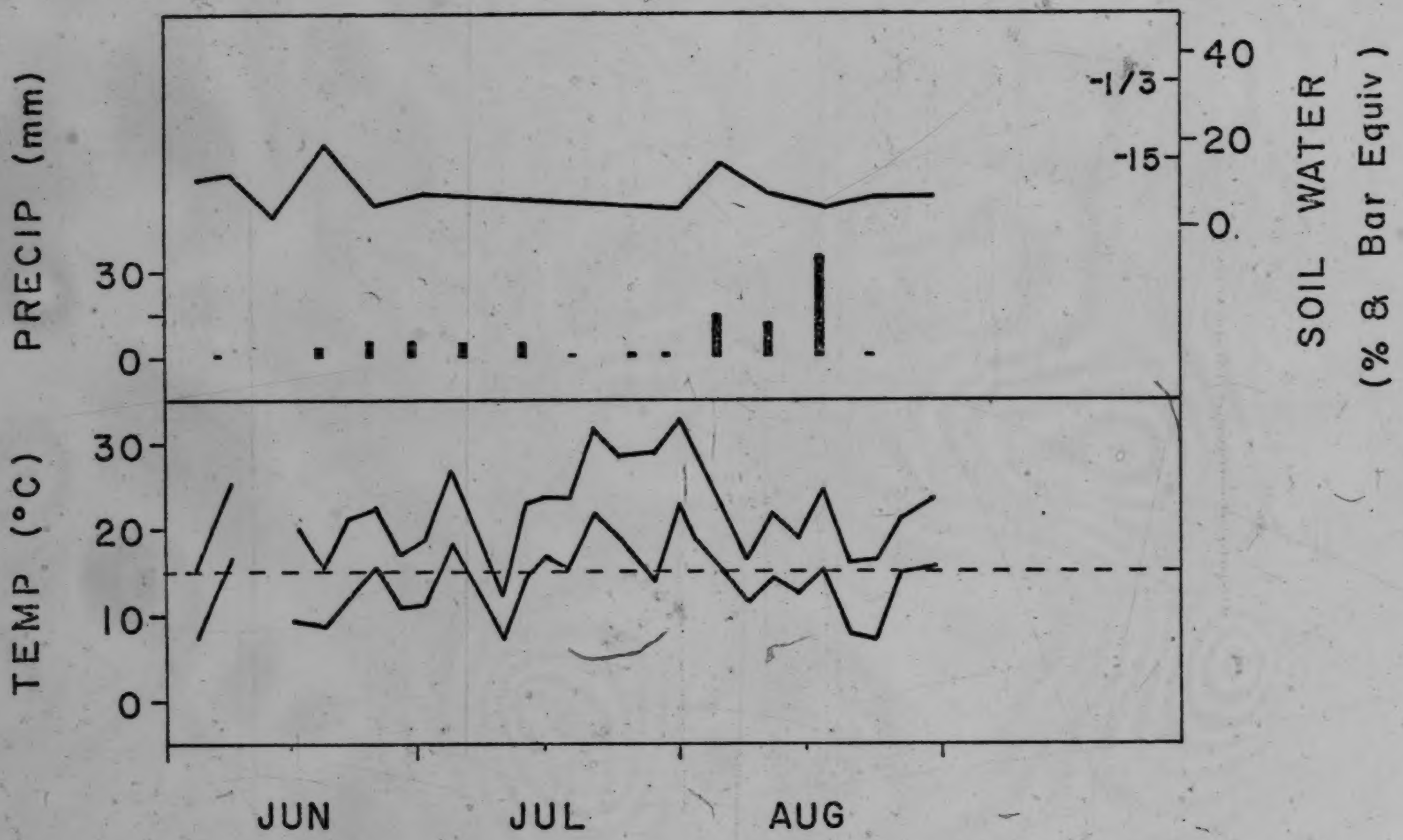

Figure 31. Environmental data from Site S hummock top microsite for 1976. In the top graph the line is soil water content and bars are six day sums of precipitation. In the lower graph the lines are three day means of maximum temperature (upper) and daily mean temperature (lower).

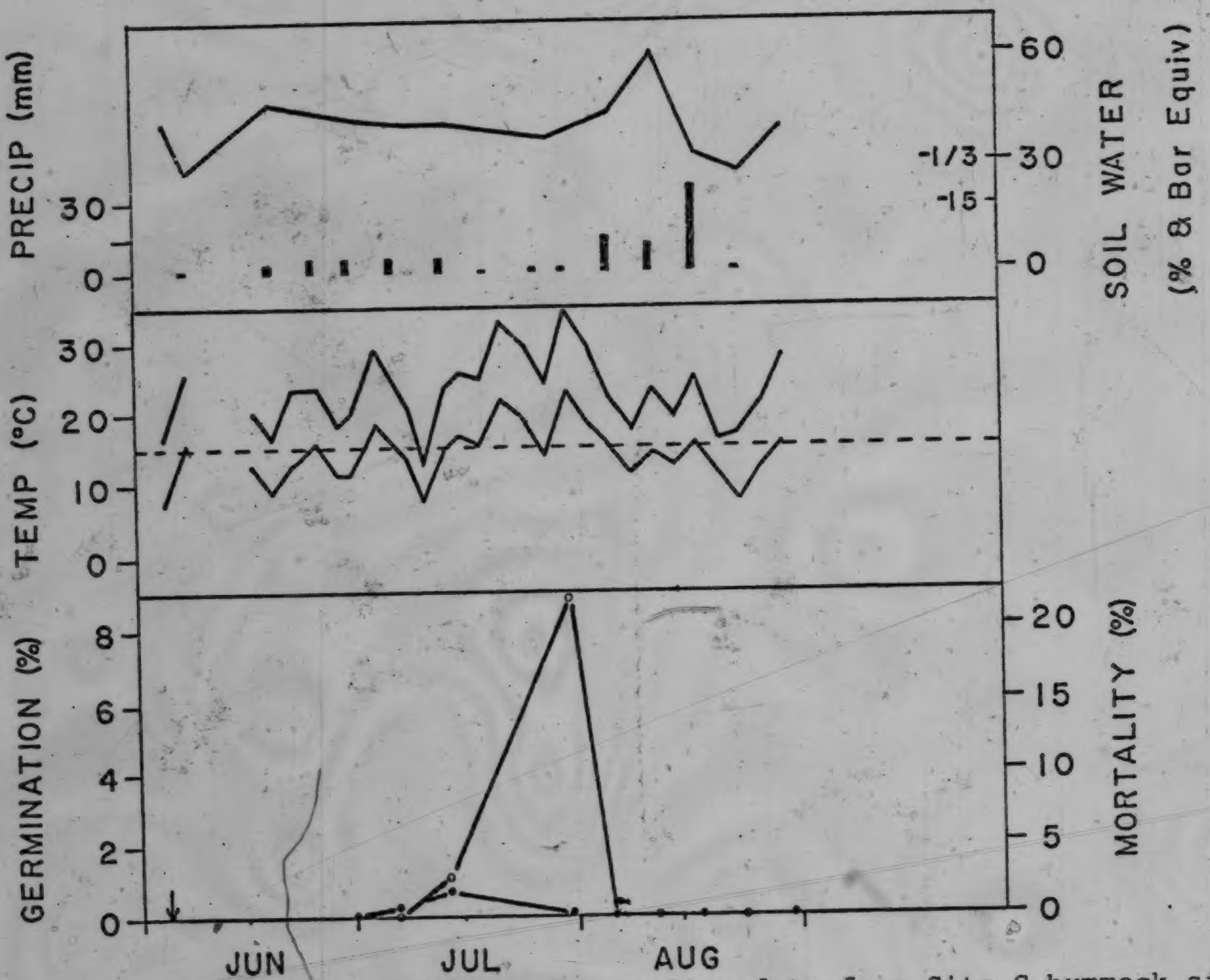

Figure 32. Environmental, germination and mortality data from Site S hummock side microsite for 1976. In the top graph the line is soil water content and bars are six day sums of precipitation. In the middle graph the lines are three day means of maximum temperature (upper) and mean daily temperature (lower). The lower graph is germination (●), germling mortality (○) and date of sowing (↓).

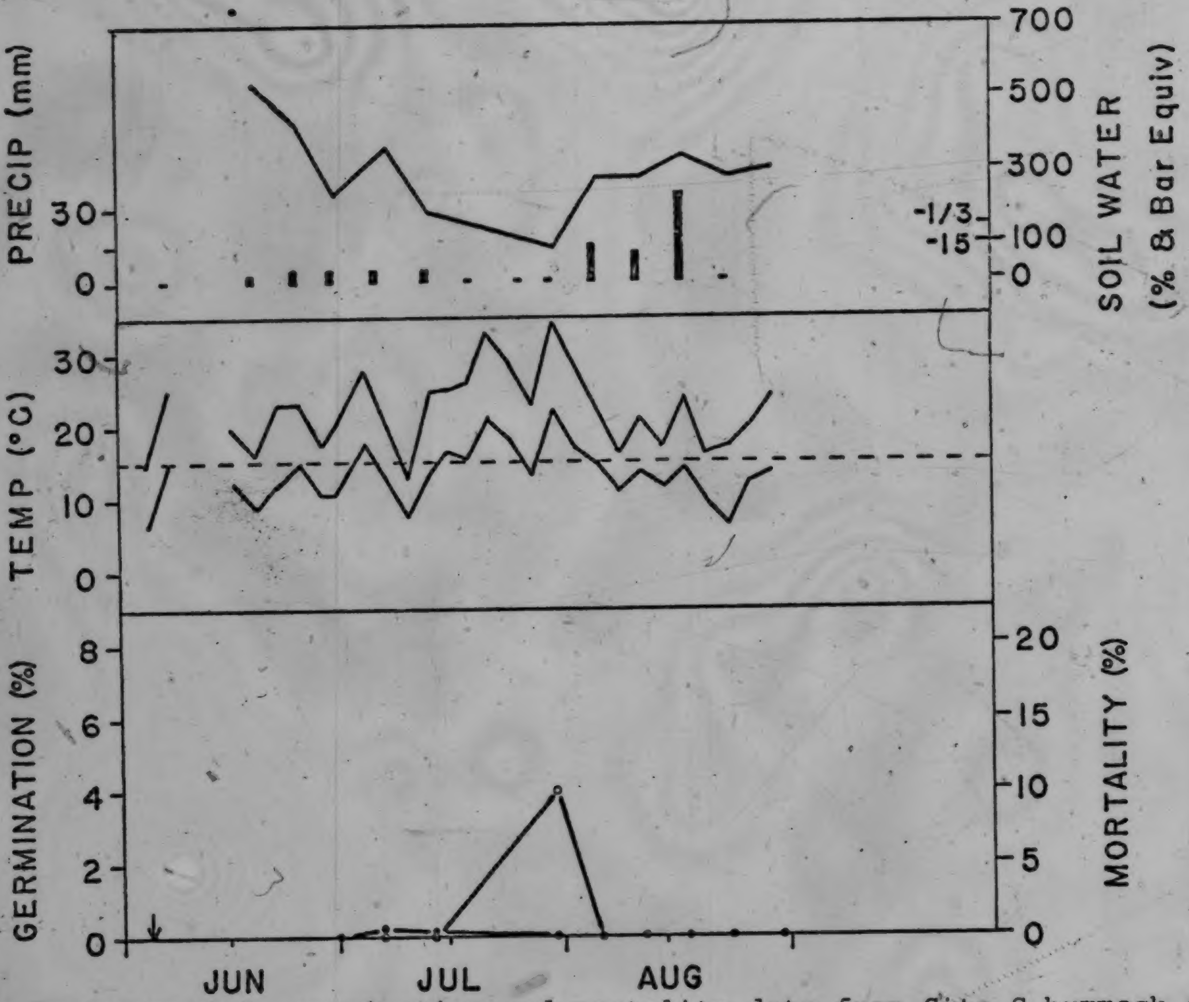

Figure 33. Environmental, germination and mortality data from Site S hummock trough microsite for 1976. In the top graph the line is soil water content and bars are six day sums of precipitation. In the middle graph the lines are three day means of maximum temperature (upper) and mean daily temperature (lower). The lower graph is germination (●), germling mortality (o) and date of sowing (↓).

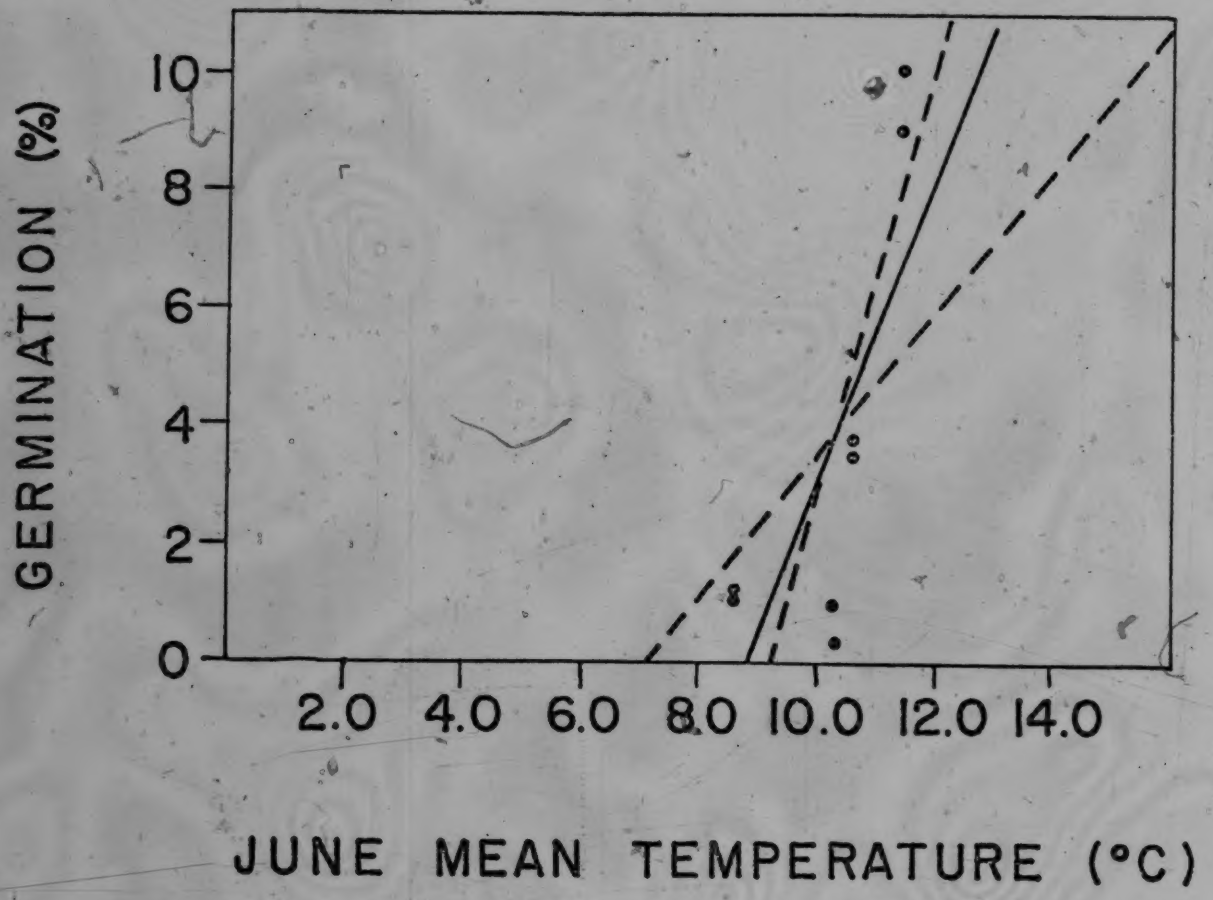

Figure 34. Field germination as a function of June mean temperature for *Picea mariana*. Solid line is a least squares fit to the data. Dashed lines are 80% confidence limits of the slope.

Table 14. Germination field trials by microsite for *P. mariana*, 1975.

Site N side microsite

Factor	DF	MS	F	Probability
Replicates	5	0.00028	0.96	Non-sign
Treatment	12	0.01200	43.94	P<0.001
Error	60	0.00029		
Total	77			

Site N trough microsite

Factor	DF	MS	F	Probability
Replicates	5	0.00047	0.29	Non-sign
Treatment	12	0.00604	3.75	P<0.001
Error	60	0.00161		
Total	77			

Site S side microsite

Factor	DF	MS	F	Probability
Replicates	5	0.0012	1.94	Non-sign
Treatment	12	0.0309	50.06	P<0.001
Error	60	0.00062		
Total	77			

Site S trough microsite

Factor	DF	MS	F	Probability.
Replicates	5	0.0031	1.67	Non-sign
Treatment	12	0.0299	16.16	P<0.001
Error	60	0.0018		
Total	77			

correlated with germination, due to early July germination dates.

Table 15. Percent germination and mortality for Site N side and trough microsites in summer 1975 and winter 1975-76 with non-significant ranges (P=0.05).

	1975													1976
	June		July					August				Sept		June
	14	30	6	10	16	22	28	2	8	14	20	27	28	2
Germ. (%)	sown	0												
Germ. (%)	sown	0	2.2	0.9	0.3	0	0.1	0	0	0	0	0	0	0
non-sign.		—	·	·	·	—	—	—	—	—	—	—	—	—
Mort. (%)		0	0	9.7	16.1	12.2	7.8	9.2	0	6.9	1.5	0	0	0
non-sign				—	—	—	—	—	·	—				
ranges				—	·	·	—	—	·	—	—			
		—	—	·	·	·	—	—	—	—	—	—	—	—
trough msite														
Germ. (%)	sown	0	0.3	0.4	1.5	0.2	0.3	0.5	0.3	0.3	0	0.1	0	0
non-sig ranges		—	—	—	·	—	—	—	—	—	—	—	—	—
Mort. (%)		0	0	0	1.4	0	0	0	0	2.1	0	0	0	19.6
non-sig. Ranges		—	—	—	—	—	—	—	—	—	—	—	—	

Table 16. Percent germination and mortality for Site S side and trough microsites in summer 1975 and winter 1975-76 with non-significant ranges. (P=0.05)

	1975													1976
	June		July						August				Sept	June
	12	29	3	8	14	19	24	30	5	11	17	27	28	2
Side msite														
Germ. (%)	sown	0	4.4	3.0	1.2	0.4	0.1	0	0	0	0	0	0	0
non-sign. ranges		___	.....	.....	.....	___	___	___	___	___	___	___	___	___
Mort. (%)		0	0	6.7	9.4	6.9	1.4	1.6	0.8	0	1.5	0	0	0
non-sign. ranges		___	___	___	___	___	___	___	___	___	___	___	___	___
Trough msite														
Germ. (%)	sown	0	2.2	5.0	2.3	0.3	0.3	0	0.1	0	0	0	0	0
non-sign. ranges		___	___	....	___	___	___	___	___	___	___	___	___	___
Mort. (%)		0	0	4.2	25.2	20.9	4.7	2.8	1.2	0	1.0	0	0.4	0.5
non-sig. ranges		___	___	___ ___	___	___	___	___ ___	___ ___	..... ___	___ ___	..... ___	..... ___	___ ___

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Table 17. Germination field trials by microsite for *P. mariana*, 1976.

Site N side microsite

Factor	DF	MS	F	Probability
Replicates	5	0.00136	1.65	Non-sign
Treatment	8	0.00215	2.60	P<0.025
Error	40	0.00083		
Total	53			

Site N trough microsite

Factor	DF	MS	F	Probability
Replicates	5	0.00039	0.47	Non-sign
Treatment	8	0.00234	2.80	P<0.025
Error	40	0.00083		
Total	53			

Site S side microsite

Factor	DF	MS	F	Probability
Replicates	5	0.00059	1.18	Non-sign
Treatment	8	0.00366	7.35	P<0.001
Error	40	0.00050		
Total	53			

Site S trough microsite

Factor	DF	MS	F	Probability
Replicates	5	0.00065	1.69	Non-sign
Treatment	8	0.00052	1.34	Non-sign
Error	40	0.00039		
Total	53			

Interpreting soil water relations data was confusing due to the necessity of composite soil samples. Soil water reductions to unavailable ranges (-15 bar) in the seed bed (top 1 mm?) were not reflected in the small changes in soil

Table 18. Percent germination and mortality for Site N side and trough microsites in summer 1976 with non-significant ranges (P=0.05)

	June 5	June 29	July 5	July 11	July 29	August 4	August 11	August 16	August 22	August 30
Side msite										
Germination (%)	sown	0	0.2	0.4	0.4	0.1	0.1	0	0	0
non-significant ranges										
Mortality (%)	0	0	0	2.8	0	8.3	0	0	0	0
non-significant mortality										
Trough msite										
Germination (%)	sown	0	0.3	0.2	0.5	0	0.1	0	0	0
non-significant ranges										
Mortality (%)		0	0	0	3.3	0	0	0	0	0
non-significant mortality										

Table 19. Percent germination and mortality for Site S side and trough microsites in summer 1976 with non-significant ranges (P=0.05).

	June			July				August		
	4	1	7	13	30	5	11	17	23	29
Side μsite										
Germination (%)	sown	0	0.2	0.7	0.1	0	0	0	0	0
non-significant ranges										
Mortality (%)		0	2.8	56.8	0	0	0	0	0	0
non-significant ranges										
Trough μsite										
Germination (%)	sown	0	0.3	0.2	0.5	0	0.1	0	0	0
non-significant germination										
Mortality (%)		0	0	0	10.0	0	0	0	0	0
non-significant mortality										

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water content in the 0-2.5 cm sample; therefore seed germination was probably prevented by low soil water, well before water contents equivalent to -1/3 bar were measured. Soil water status probably determined the cessation of germination after mid-July or prevented germination when temperature was not limiting. Surface (0-2.5 cm) soil water content was lower than -15 bar on all hummock tops throughout 1975 and 1976 only reaching levels of available soil water immediately after precipitation or snow release (Figures 22, 25, 28 and 31). The absence of germination on hummock top microsites therefore was the result of unavailable soil water. Snow melt appears to be the only major source of recharge as no discernible difference was detected in microsite soil water content between 1975 and 1976, though June 1976 precipitation was double average values. Germination in 1976 was significantly reduced ($P<0.01$) from 1975 values in spite of increased precipitation. The interaction of temperature and soil water was critical for germination of P. mariana. Microsite temperatures must average more than 15°C before measureable reduction in soil water content occurs (before 15 July). Laboratory germination trials required 6-10 days for radical elongation, suggesting temperature requirements must be met before 1 July. These requirements were not met in 1976, resulting in reduced germination.

Overwintering of viable seeds and a few successful germinations (10) were found, suggesting destruction of the majority of ungerminated seed. This apparent destruction of *P. mariana* seed supported earlier laboratory germination work and literature reports (Fraser 1976).

Mortality

Significant components of variance were found in the interaction of regional site, microsite and time producing mortality in the 1975 and 1976 germling populations (Tables 20 and 21). Individual microsites, however, did not experience significant differences in mortality in 1976 (Table 22, 18 and 19) apparently due to low germination and were dropped from consideration. Mortality percentages did not differ in the microsites after one year (Table 23) but two mortality patterns were apparent (Fig. 35). Both microsites at Site S and the side microsite, Site N show low initial probabilities of 15 day survival (.68) compared to the Site N trough microsite (.96). Reduced trough microsite mortality was the result of cooler temperature and high soil water contents (Fig. 24). All summer mortality resulted from water stress induced by high transpiration stress (see physiology section), heat stem girdling as found in other conifers (Baker 1927) or reduced soil water. Summer percent mortality peaked 16 July and 14-19 July (Site N and S, respectively, Tables 24, 15 and 15) following three day means with maximum temperatures greater than 30°C at +5 cm. Minor mortality peaks occurred before 14 August (Site N) and

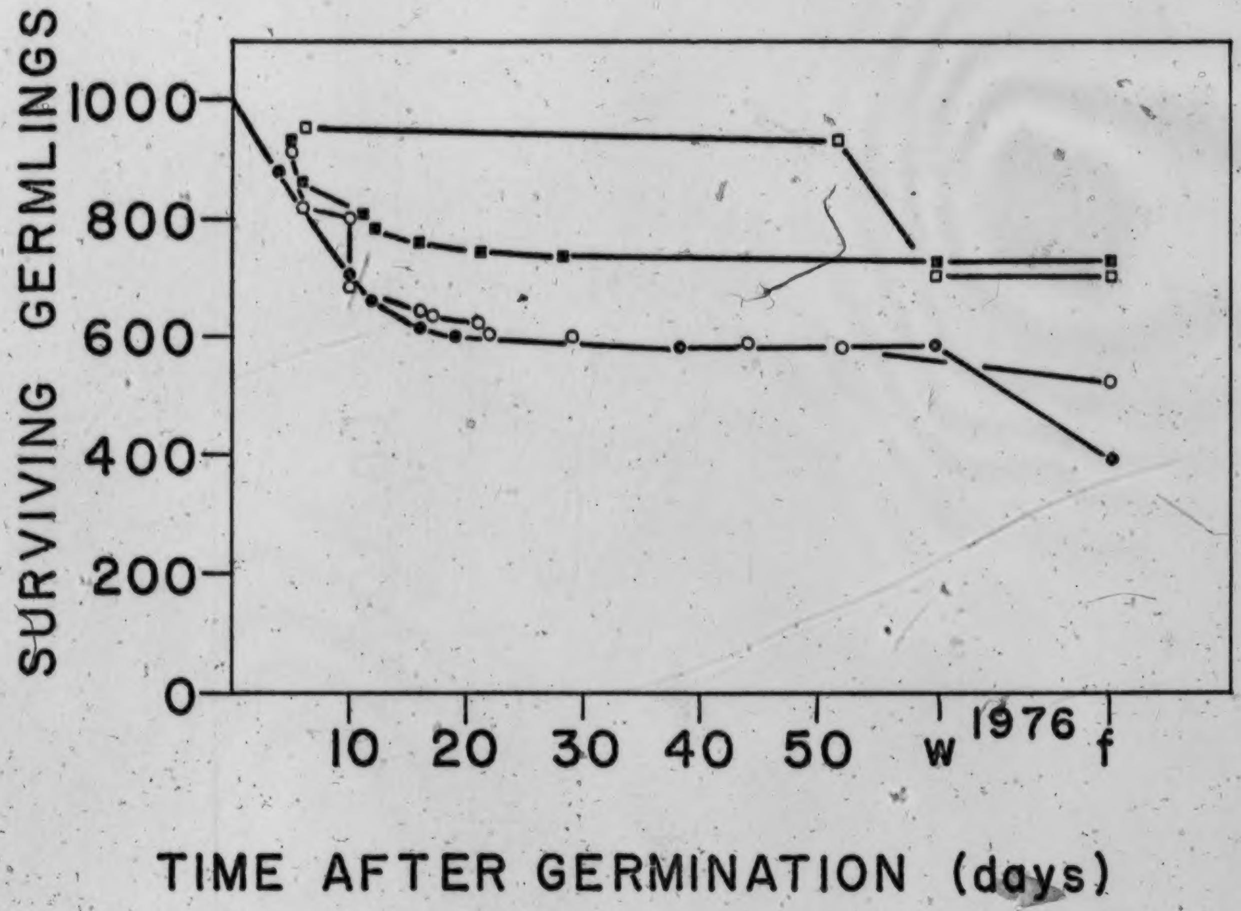

Figure 35. Survivorship curves for 1975 germlings (●=Site N side microsite; □=Site N trough microsite; ■=Site S side microsite; ○=Site S trough microsite).

Table 20. Complete factorial analysis of variance for field mortality of *P. mariana* germlings in 1975.

Factor	DF	MS	F	Probability
Replicates	5	0.0097	0.96	non-sign
Interaction SiteXMsiteXTime	24	0.0558	5.50	P<0.001
Error	385	0.0101		
Total	467			

Table 21. Complete factorial analysis of variance for field mortality of *P. mariana* germlings in 1976.

Factor	DF	MS	F	Probability
Replicates	5	0.0033	0.32	Non-sign
Interaction SiteXmsiteXtime	16	0.0644	6.12	P<0.001
Error	265	0.0105		
Total	323			

17 August (Site S) associated with 24-31°C and 33-42°C microsite maximum temperatures, respectively. Precipitation (up to 15 mm) only temporarily reduced mortality (i.e. 8 August 1975, Site N and 11 August 1975, Site S) probably through reduction in temperature rather than increasing soil water.

Overwintering mortality was significant only in the trough microsite (Site N). Abundant needle ice formation as observed 28 September 1975 resulted in burial or uprooting of germlings and high (20%) spring mortality (Fig. 24). High

Table 22. Complete factorial analysis of variance for individual microsite germling mortality for 1976.

Site N side microsite

Factor	DF	MS	F	Probability
Replicates	5	0.0123	0.88	Non-sign
Treatment	8	0.0132	0.82	Non-sign
Error	40	0.0150		
Total	53			

Site N trough microsite

Factor	DF	MS	F	Probability
Replicates	5	0.0040	1.0	Non-sign
Treatment	8	0.0040	1.0	Non-sign
Error	40	0.0040		
Total	53			

Site S side microsite

Factor	DF	MS	F	Probability
Replicates	5	0.0313	1.08	non-sign
Treatment	8	0.4646	16.07	Non-sign
Error	40	0.0289		
Total	53			

Site S trough microsite

Factor	DF	MS	F	Probability
Replicates	5	0.0145	1.00	Non-sign
Treatment	8	0.0145	1.00	Non-sign
Error	40	0.0145		
Total	53			

---

soil water content of this microsite reduced summer mortality but promoted needle ice production thereby increasing overwinter mortality.

Table 23. Mortality summaries of P. mariana for summer of 1975 and winter 1975-76.

ANOVA for mortality of all microsites

Factor	DF	MS	F	Probability
Replicates	5	0.0990	1.19	Non-sign
Treatment	3	0.2147	2.59	Non-sign
Error	15	0.0830		
Total	23			

Percent mortality for all microsites

	Site N		Site S	
	Side	Trough	Side	Trough
Percent mortality	55.0	25.8	32.7	57.7

Grand mean 42.8%

Minor sources of mortality (non-significant) were mechanical damage by snowfall (2 August 1975), inability to penetrate soil, uprocting or burial by rain splash and grazing (insect?). Germling submergence (snowmelt to 5 June 1976, in the trough microsite, Site N) resulted in no observed short term mortality indicating some resistance to waterlogging. Germination time had no significant affect on mortality of subpopulations divided a posteriori at 8 July (Site S), 10 July (Site N, side microsite) and 16 July (Site n, trough microsite). Germling age and daily microenvironment apparently were the determining mortality controlling factors. Germination time or microsite had no

Table 24. Complete factorial analysis of variance for *P. mariana* germling mortality in individual microsites, 1975.

Site N side microsite

Factor	DF	MS	F	Probability
Replicates	5	0.0132	1.38	non-sign
Treatment	12	0.0593	6.23	P<0.001
Error	60	0.0164		
Total	77	0.0095		

Site N trough microsite

Factor	DF	MS	F	Probability
Replicates	5	0.0085	0.52	non-sign
Treatment	12	0.1668	10.17	P<0.001
Error	60	0.0164		
Total	77			

Site S side microsite

Factor	DF	MS	F	Probability
Replicates	5	0.0375	1.34	non-sign
Treatment	12	0.1004	3.58	P<0.001
Error	60	0.0281		
Total	77			

Site S trough microsite

Factor	DF	MS	F	Probability
Replicates	5	0.0033	0.49	non-sign
Treatment	12	0.0809	11.93	P<0.001
Error	60	0.0068		
Total	77			

effect on germling success, suggesting initial germination was the major determinant of stand reproduction.

3. Discussion

Temperature limitation of P. mariana probably would prevent germination entirely (assuming viable seed) in Region I, and would probably reduce germination in Region II to one percent in average years. Therefore Inuvik June mean temperature (10°C) would not insure reliable germination of P. mariana. Evidences from 1975 were that germination was reduced (9.6% to 3.6%, Site S and N, respectively) over 40 Km distance between Site N and S. This was in response to Inuvik above average temperature (11.3 to 10.5°C), Site S and N). Germination in 1976 was also limited (0.6% and 1.2% germination not significantly different, Site S and N, respectively), the result of slightly above average (10.3°C, Site S) and below average (8.9°C, Site N) temperatures. Similar annual differences in field germination were reported by Pace (1955), but were not attributed to an environmental factor.

A reliable and suitable environment for germination becomes important in consideration of the short (5-8 year) post-fire period for establishment of P. mariana. This short period is the result of rapid seed release after fire (Wilton 1963), apparently short seed longevity (see germination section) and destruction of seed in the soil (this study; Johnson 1975; Fraser 1976). Narrow seedling age distributions (Fig. 37) supportive of these observations were also found by Ahlgren (1959) and Wein (1975).

Germination was found constant between differing seed beds only by Jarvis(1966) in Manitoba and in this study. This may be the result of temperature limitations as most studies report differing germination success with different seed beds (Ahlgren 1959, Lebarron 1948, Pace 1955, Vincent 1965). Mineral soil or "moist moss" seed beds are generally favored by _P. mariana_ and most authors report improved seed bed conditions with burning. Only Johnston (1967 in Zasada 1971) reported reduced germination on burned surfaces.

Timing of _P. mariana_ germination in response to high soil temperatures and favorable water relations was similarly reported by Pace. Eis (1967) working with _Picea englemannii_ and _Abies lasiocarpa_ reported a similar timing (1 July to 16 July) to this study, suggesting also the importance of temperature and soil moisture interactions to other species. No author reported that germination increased with precipitation events and Arnott's (1973) review suggested germination was best when sowing of pine and spruce seed occurred within 3-4 weeks after snow melt supporting the importance of winter recharge of the soil system.

One year survivorship was similar (.60 to .41%) in all reported seed beds (Ahlgren 1959 and Pace 1955) with only Jarvis (1966) reporting unusually low survivorship (.075).

Table 25. Summaries of germination and establishment for *P. mariana* near Inuvik and literature values.

Location	Viability	Estab/seed Total	Estab/seed Viable	germ/viab
1975 Site N	33%	1/45	1/15	11%
Site S		1/17	1/6	29
1976 Both Sites		1/104	1/37	3
Jarvis (1966) Manitoba	85%			
Litter		1/200	1/170	19%
Amorphous organic		1/50	1/43	30
Mineral soil		1/40	1/34	19
Zasada (1971)				
Johnston Minnesota	95%			
Litter		1/4.5	1/4.3	
Compacted		1/3.4	1/3.3	
Scalped		1/5.6	1/5.3	
Burned		1/47	1/50	
LeBarron (1948) Minnesota				
Mineral		1/3.2		
Scarified & shaded		1/16		
Burned		1/25		
Undisturbed		1/100		
Place (1955) New Brunswick	72%			
Ranges estimated from data		1/8	1/6	42%
		1/10	1/7	35
		1/16	1/11	21
		1/34	1/24	10
		1/40	1/28	8

Survivorship in *Picea englemannii* and *Abies lasiocarpa* (Eis 1967) was also comparable (.55 and .60, respectively) with a similar observation that mortality was high during the first few weeks after germination. All authors cite water stress and heat girdling as primary causes of mortality with no mention of winter damage by needle ice. Only Pace referred to overwinter mortality.

Seedling to seed ratios (Table 25) summarize both environmental and seed viability effects on seedling success compared to other studies. The role of temperature in germination reduction became apparent in the ratio of established one year-old seedlings to viable seed and the percent field germination of viable seed. This comparison removes the effects of low germination potential for the Inuvik population and reveals not only annual and geographical temperature limitations in this study but also reductions compared to other reports.

The comparable mortality rates of the Inuvik germlings to other studies infers that the success of establishment (or lack thereof) would be dependent on seed viability and the germination limits imposed by low spring temperatures. These characteristics of _P. mariana_ and their other environmental interactions shown in the 1975 and 1976 studies suggest little or no regeneration would occur after a fire in Regions I and II.

VI. TREE GROWTH

1. Methods

Growth measurements across treeline were made using three replicate 10 X 10 m plots at each sampling site. Density, height, diameter at breast height (DBH) and diameter at the stem base (BD) measurements were made on each tree (>1 m in height) and counts made of small individuals (<1 m). Counts included all rooted stems which displayed apical dominance, including vegetative reproduction (layering). Heights were measured using an Abney level and all diameters were measured with calipers.

Tree age was determined by sectioning and counting rings in the laboratory under a binocular dissecting microscope. Six (or more) trees were sectioned at each site spanning the range in sizes from greater than 1 m to canopy dominants. Seedling ages in young stands were determined by counts of terminal bud scars, including years buried by peat, to the cotyledons (Fig. 36). Stand origins were dated using burn scar ages collected at stand margins.

Cone production was counted from 87 trees felled for either stand age or burn scars. All cones in the top 2 m of the crown mere separated into 1, 2-5 and 5+ year-old classes in the laboratory based on branch position relative to the branch bud. Seeds per cone were determined by dissection.

Figure 36. Twenty-six year old seedling showing initiation of adventitious roots at terminal bud scars. Pen points to position of cotyledons now 13cm below peat surface.

2. Results

Seedling age distributions (Fig. 37) suggest stand reproduction only immediately after burning. Section ages however, suggest a much broader age distribution with 10 to 80 year discrepencies between ages and burn dates. These discrepancies and increases in age variation were the result of lost annual rings due to burial by peat, suppressed growth and/or confusion caused by layers. Though these errors would be highly variable between trees, a linear correction (r=0.9871, n=24) based on the oldest ring counts in a stand and fire scar sections was developed and applied to all stand ages in the study. This correction was:

$$A=16.9764+1.0926SA. \qquad (1)$$

Where A is the age of the stand (since burning) and SA is the section age of the oldest stand members. A single corrected stand age was used for all stand members and the assumption made that all individuals were the same age (±8.8 years, SE of estimate).

Stand density was a function of age (Fig. 38) decreasing to a relatively constant stand density (ca 6000 trees ha^{-1}) by 80 years in age. Density subsequently increased after 200 years. This increased density resulted from the death and windthrow of dominant trees and increased layering. Density increases were not the result of seedling establishment. Layering appeared sufficient to effect stand replacement in the absence of burning.

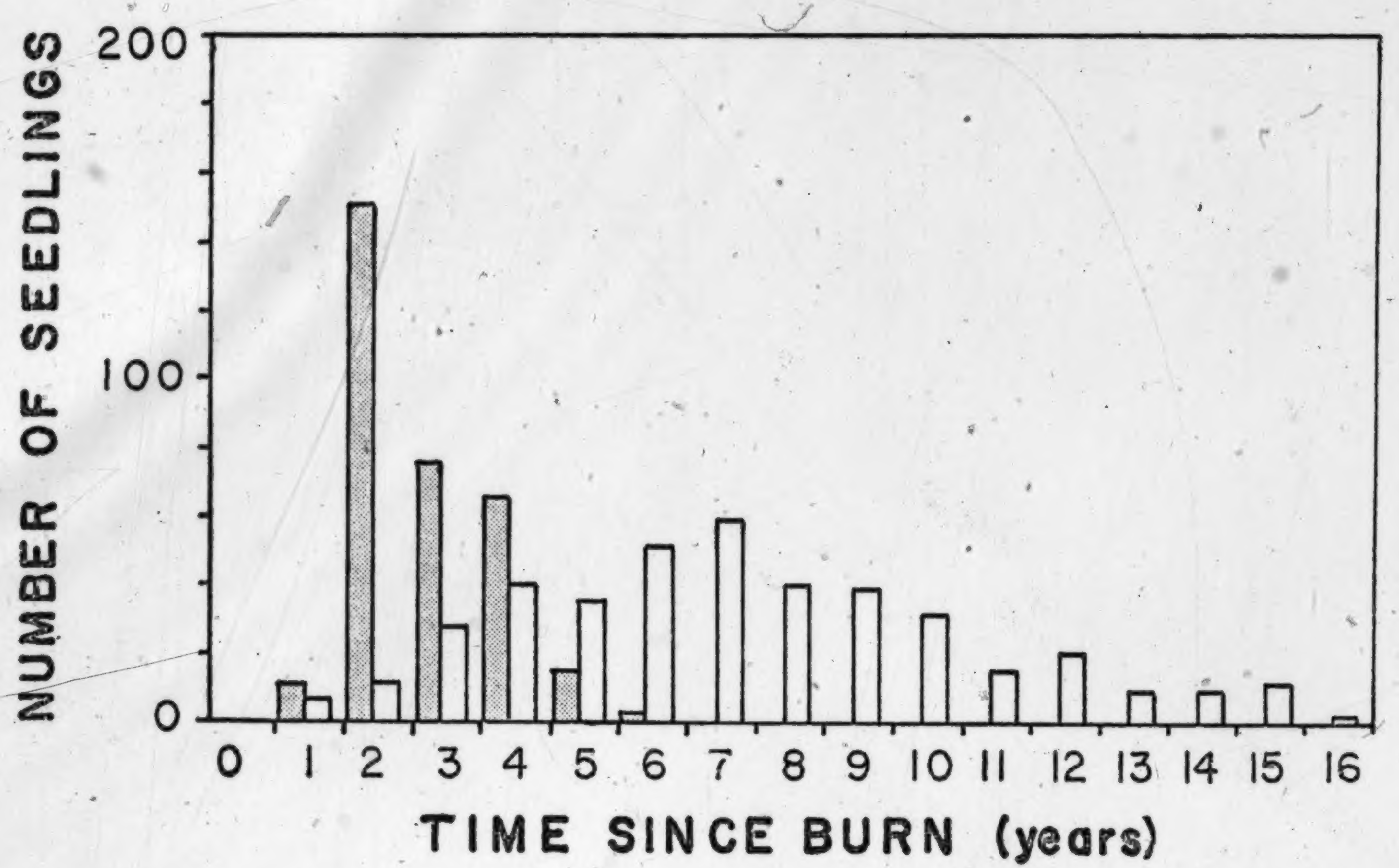

Figure 37. Age distributions of two stands of seedlings. Shaded bars are from Site S, 1968 burn. Open bars are from Site IIIh, 1947 burn and show increasing error in measurement of age.

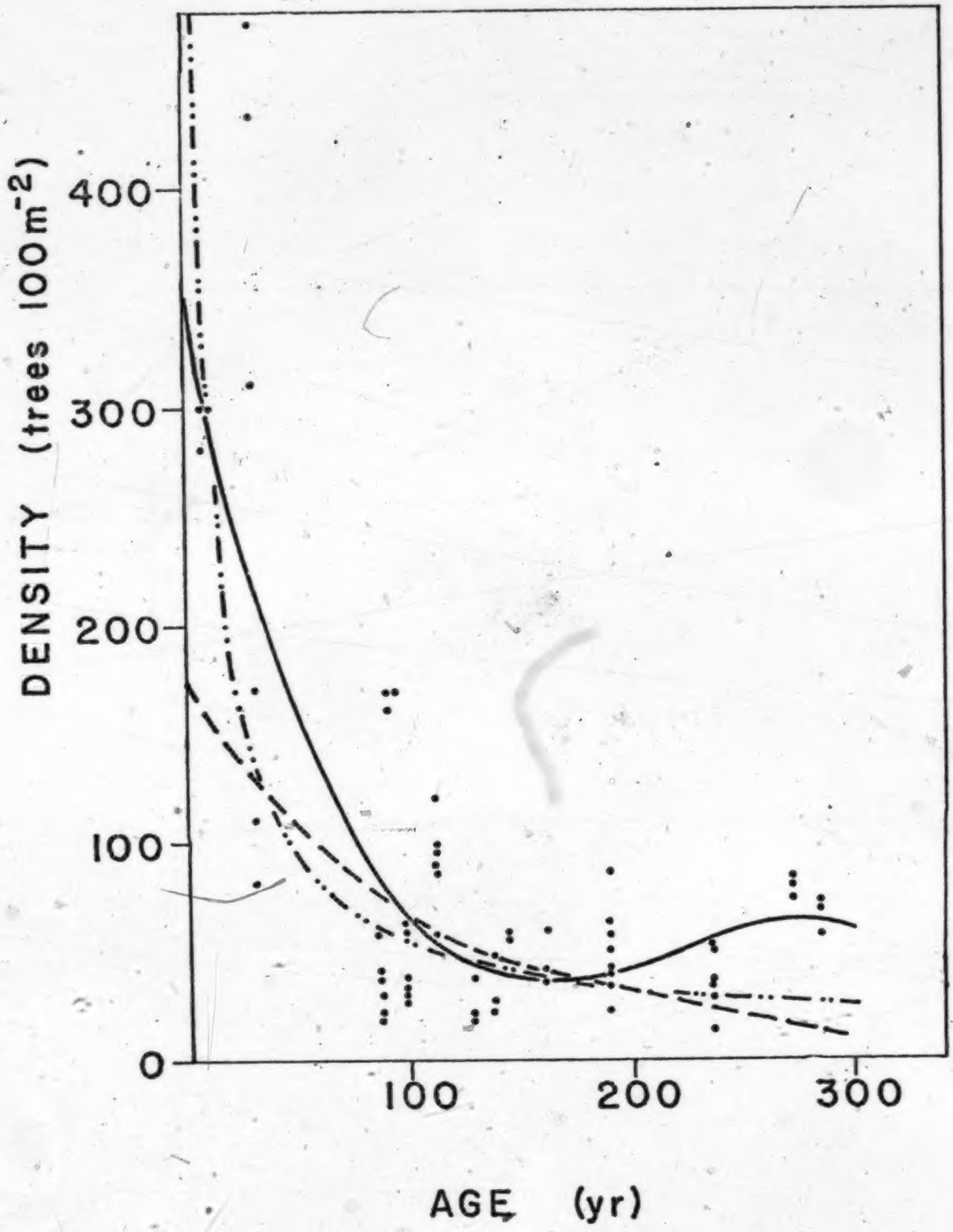

Figure 38. Tree density as a function of age for all stands sampled. Solid line is a polynomial curve fit. Dotted and dashed line is a power function fit. Dashed line is a negative exponential fit. Data points are individual plot values.

Assuming similar patterns of mortality for all stands studied, tree survivorship could be described by one of two possible models (Hett 1971). One was the negative exponential model:

$$Yt=Yo\ e^{-bx}. \tag{2}$$

Where Yt is the number of plants per unit area at time t, Yo is the initial number of plants, b the mortality rate and x is age in years. This model assumes mortality was constant through time and was rejected for that reason. The power function model:

$$Yt=Yo\ X^{-b} \tag{3}$$

assumes mortality rates change with time and was felt more appropriate. This model transformed and fitted to the data from stands less than 200 years old by a least squares technique gives the relationship:

$$\ln Yt=7.3606-0.7246 \ln X \tag{4}$$

describing density as a function of age. This relationship (equation 3) fitted to the data, though not significantly different from the previous example (equation 2) by a Z test (Sokal and Rolf 1969), nevertheless described a more highly correlated ($r=-0.7052$ vs. -0.6147, $n=47$) relationship.

Growth was examined from two points, volume growth ($V=1/3\ r^2h$) and height growth. Mean volume was calculated for each plot and the effect of stand density, latitude and age examined by stepwise linear multiple regression of the form:

$$Y=a+b_1 x_1 +b_2x_2+....b_nx_n \qquad (5)$$

Where Y is the dependent variable, a is the intercept, b_1 to b_n are partial regression coefficients and x_1 to x_n are the independant variables (Steele and Torrie 1960).

The age squared term produced a curvilinear relationship simulating the senescence of the stand with age (Fig. 39). Density accounted for 71% of the explained variance though the magnitude of the standardized partial regression coefficient was 33% stand age (Table 26). Density reduced mean tree volume, both as related to young dense stands and to overstocked older stands. An investigation of log mean tree volume as a function of log density yielded a significant negative correlation (r=-0.5704, n=44) suggesting intraspecific interference resulting in stand thinning (Fig. 40). The slope of the thinning relationship

Table 26. Stepwise multiple regression statistics for log mean tree volume along the study transect ($x10^3$ cm^3) n=53.

Indep. variable	Partial regress. coefficient	Stand. partial regress. coef.	t	R^2
Intercept	90.1897			
Density	-0.008531	-0.5457	-5.2	0.5754
Latitude	-1.3346	-0.4360	-6.7	0.7275
Age^2	-0.00006575	-1.6392	-4.4	0.7441
Age	0.02163	1.6418	-4.1	0.8106

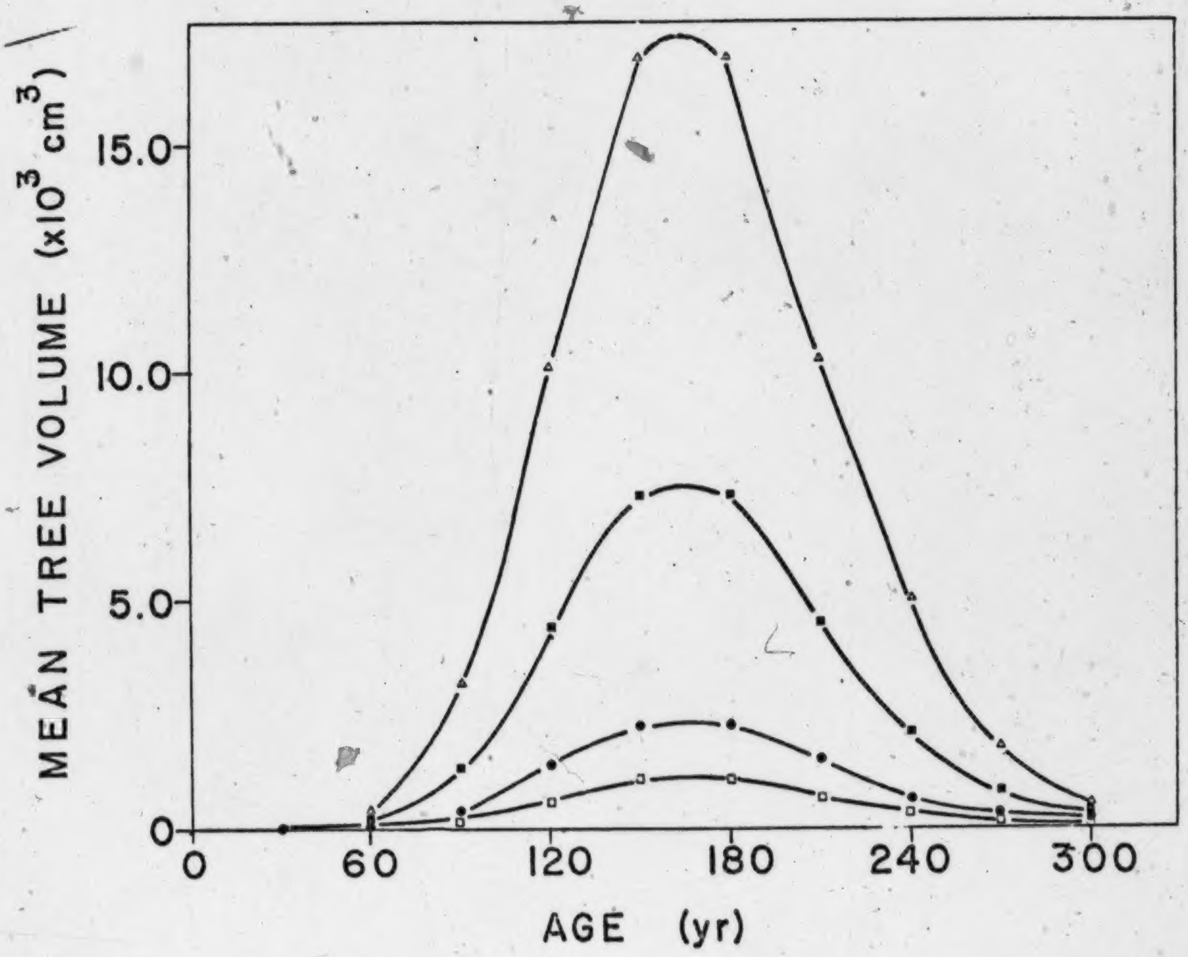

Figure 39. Mean volume of black spruce boles predicted from multiple regression of density, age and latitude. Average density for a given age was used (□=Site Ia; ●=Site N; ■=Site S; △=Near Arctic Red River).

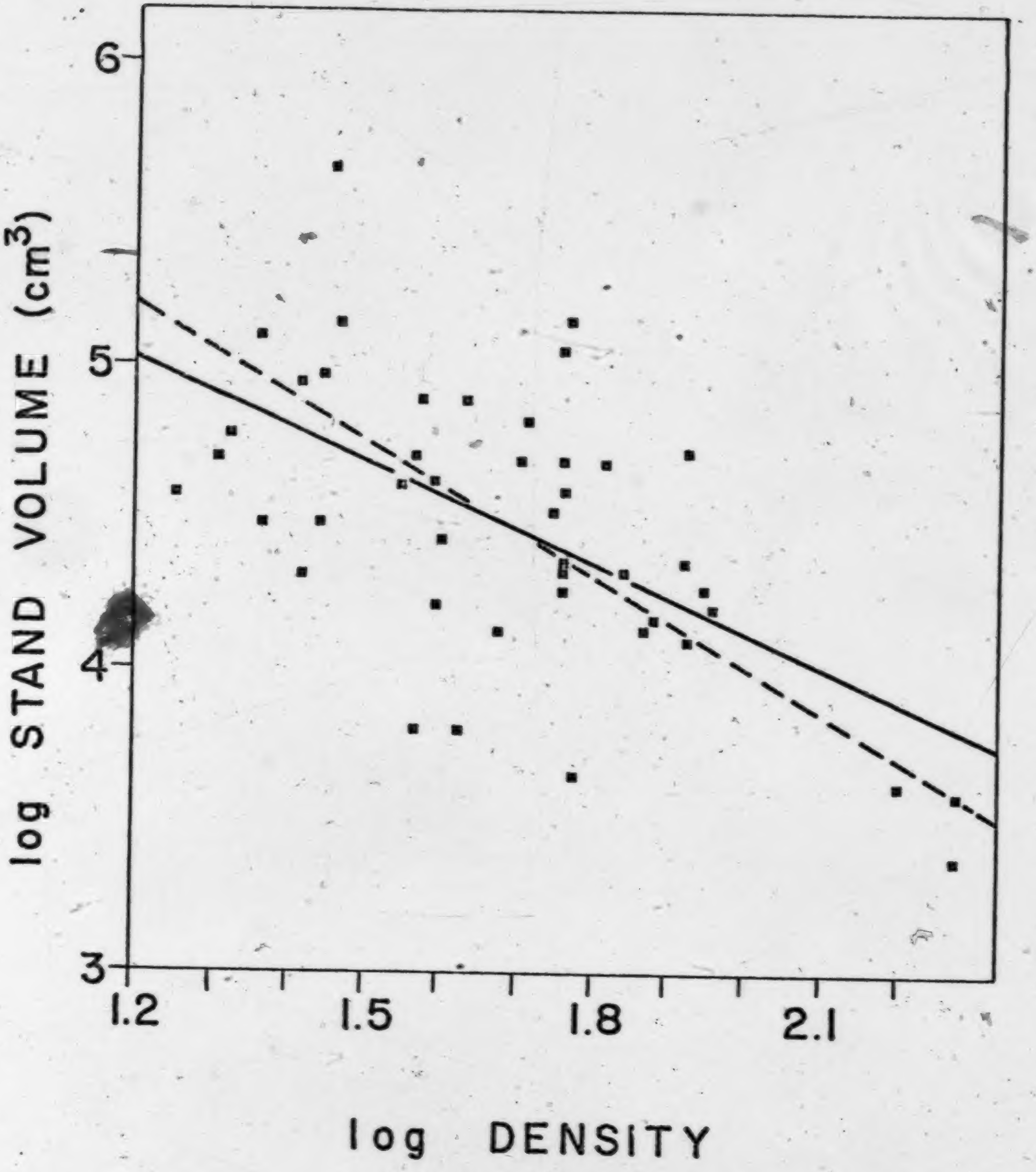

Figure 40. Least squares fit to stand thinning of *Picea mariana* along the study transect. Solid line is the least squares fit. Dashed line is the theoretical -3/2 slope.

was not significantly different from the theoretical relationship (-3/2, White and Harper 1970).

Increased latitude (decimal latitude, i.e. 68°30'=68.5°) reduced mean volume as expected in a negative manner. A similar magnitude standardized partial regression coefficient was found with both latitude and density. Age had the greatest effect on the regression and was the most useful measure for prediction of stand mean volume (3X).

Stand volume tables (Table 27) were generated for each region using the mean tree volume multiple regression (Table 26) and stand density. A density function of age polynomial was developed:

Table 27. Average stand volumes by region for P. mariana predicted from the multiple regression equation and average stand density ($m^3\ ha^{-1}$).

Age	Region				Density
	I	II	III	IV	
50	0.21	0.47	1.47	3.36	16,100
100	2.18	4.81	15.07	34.32	6,700
150	3.94	8.69	27.25	62.07	3,700
200	3.48	7.68	24.07	54.80	4,400

$$D=346.0-4.7897A+0.02351A^2-0.00003565A^3, \qquad (6)$$

where A is the stand age and D is the stand density, used to calculate average stand density. Stand volume calculated for Region I was greatly over estimated (10X) when compared to field data. These values represent a potential never reached due to physical damage by wind abrasion and lower tree densities.

Mean stand volume was linearly related (r=0.8857,n=50) to the standard deviation of stand volume by the function:

$$Y=1.58+0.98X \qquad (7)$$

X (X1000 cm^2) is the mean tree volume and Y (X1000) the standard deviation of that volume. The increasing standard deviation with mean volume resulted from the large increase in volume of a few dominants and suppression of most cohorts. These suppressed trees become the canopy with removal of dominant trees and are also responsible for layers in the understory.

Dominant height growth (mean of 6 tallest trees plot^{-1}) and average height growth of stands less than 200 years old was not predicted to be significantly different (better) using the same independant variables (age, density and latitude) than mean tree volume (R=0.8588, 0.8491 and 0.9003, n=47, 47 and 53 respectively) by a Z test.

Age accounted for most of the explained variance (89% and 88%, dominant height and mean stand height, respectively) though the magnitudes of age effects differ (Tables 28 and 29). Average stand height was less a function

Table 28. Stepwise multiple regression statistics for dominant tree heights along the study transect (m) n=47.

Indep. variable	Partial regress. coefficient	Stand. partial regress. coef.	t	R^2
Intercept	183.59858			
Age	0.02698	0.9577	7.5	0.6549
Latitude	-2.66984	-0.3617	-3.3	0.6956
Density	-0.005216	-0.2286	-2.6	0.7375

Table 29. Stepwise multiple regression statistics for average tree height along the study transect (m) n=47.

Indep. variable	Partial regress. coefficient	Stand. partial regress. coef.	t	R^2
Intercept	130.47496			
Age	0.01888	0.1407	6.9	0.6332
Latitude	-1.89951	-0.3751	-3.1	0.6670
Density	-0.0043866	-0.2767	-2.9	0.7210

of age than was stand dominant height, reflected in the magnitude of the standardized partial regression coefficient, and was probably the result of the suppressed cohort population. Dominant tree height tables were generated for each region (Table 30) using the multiple regression (Table 28) and the density polynomial (equation 6). Linear regressions of average and dominant height growth across treeline on age (Fig. 41) were calculated to provide comparative data for stands under 200 years-old.

No relationship between cone production and age was

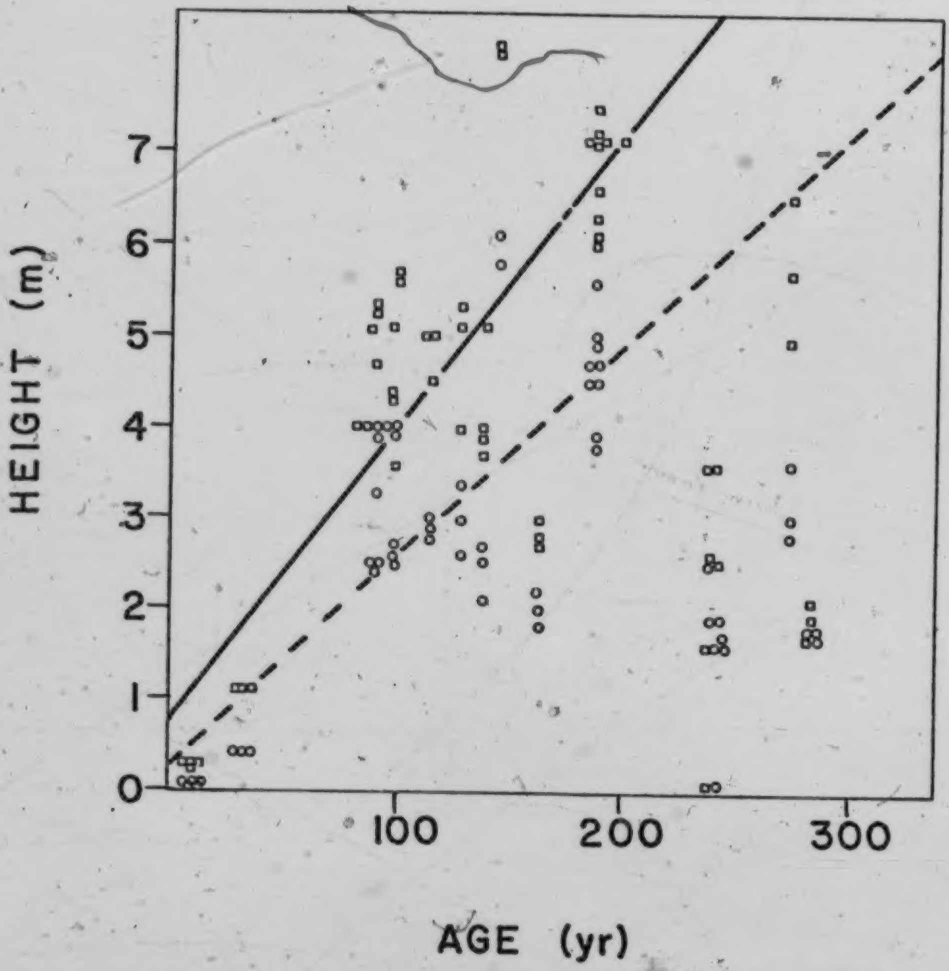

Figure 41. Average and dominant heights from Picea mariana stands under 200 years old. Solid line is regression of dominant height on age. Dashed line is the regression of average height on age (○ =average stand height; □ =dominant stand height).

Table 30. Stand dominant heights by region predicted from the multiple regression equation (Table 28) and average stand density (m).

Age	Region I	Region II	Region III	Region IV
50	0.8	1.5	2.5	3.2
100	2.7	3.4	4.4	5.1
150	4.2	4.9	5.9	6.6
200	5.5	6.2	7.2	7.9

found other than cones were first produced between 25 and 30 years and were reliably produced at 85 years. Tree volume was curvilinearily ($r=0.7537, n=69$) related to 5 year cone production by:

$$\log C=-1.1393+0.6498 \log V, \qquad (8)$$

where V is the individual tree volume and C is the number of cones 1-5 years-old. Five year cone production damped out annual variation and gives the best estimate of standing seed population. Forest-tundra (Region I) stands were not considered in the regression due to the low and sporadic cone production.

Seed number per cone varied with length by:

$$N=-1.6620+4.0690L. \qquad (9)$$

Where L is the cone length (mm) and N is the seed number. No environmental or growth characteristics could be related to cone length or seed number. Consequently, all measures of seed production used 72.8 seed cone^{-1} (±11.95 SD, n=100) in the calculation. Seed production was estimated at 6.38±2.16SD $X10^5$ ha^{-1} yr^{-1} for stands 80-100 years-old increasing to 13.2±3.00SD $X10^5$ ha^{-1} yr^{-1} for stands 150-200 years-old (Fig. 42). Stands 270+ years-old were estimated to reduce annual seed production to 6.03±1.40SD $X10^5$ seed ha^{-1} yr^{-1}. All seed production estimates were calculated from measured tree volumes and summed by plot.

3. Discussion

Even aged stands near treeline are found supporting the hypothesis that fire is central to P. mariana reproduction at treeline. Zoltai (1975) contradicts this hypothesis presenting uneven age distributions based on stem discs (+10 cm) and was apparently unaware of the associated error in sampling. The absence of P. mariana reproduction within established Inuvik stands may also be in contrast to Kershaw and Rouse's (1976) reported increased densities with age, though no separation of layered individuals was made in that study. The importance of layering was most evident in older stands where layering increased stand density and would certainly replace canopy dominant trees. Strang (1973) working between Fort Good Hope and Inuvik, reported "the open Picea forest eventually died out if fire was excluded, to be replaced by an almost tundra-like condition." He ignored the importance of layering. No evidence even in the most northerly stands (stands Ia and Ib) suggests

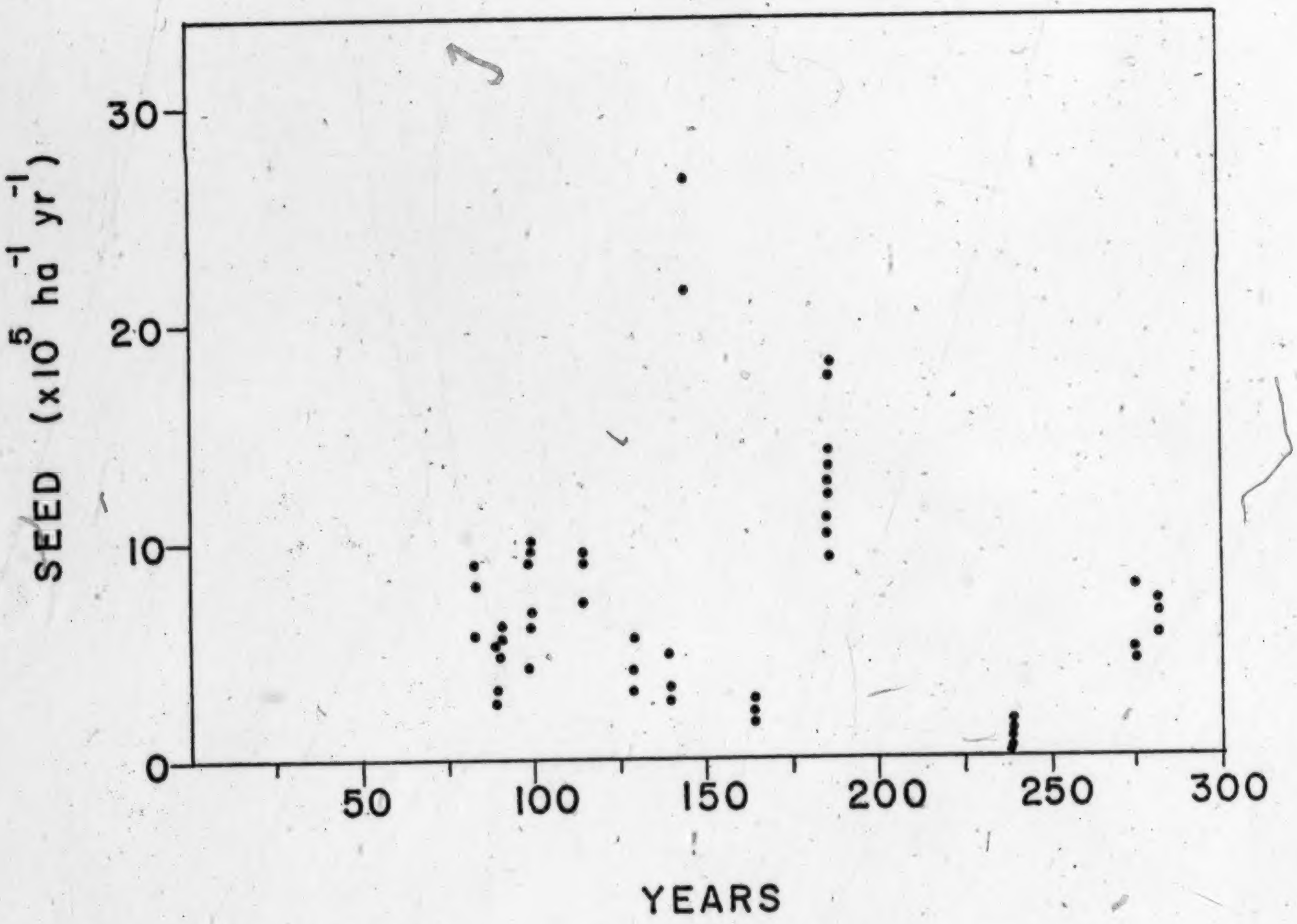

Figure 42. Estimated average annual seed production by age for sampled stands along the study transect.

elimination of P. mariana by fire exclusion.

Changing mortality rates and density dependent average tree volumes suggested intraspecific interference by P. mariana even in an open-canopy woodland community. Changing mortality rates have been found in other species both with even (Yarranton and Yarranton 1974) and uneven age distributions (Hett and Loucks 1971), but most studies have dealt with closed-canopy species. Yarranton and Yarranton suggested high initial mortality in response to limitations imposed by tree water relations as causal, but no work with thinning was presented. Further, the slope of the density dependent tree volume relationship also suggested intraspecific interference. This interference was probably through root interactions. Observations of rooting habit showed P. mariana roots primarily in the mineral soil-peat interface with certain restrictions imposed by the permafrost table (Pettapiece 1974, personal observation). Extrapolation of the power function describing mortality (0.7246 mortality rate) to the ranges including the germling survivorship experiment (0.7851 ±0.4238SD, n=4) gave results not significantly different by comparison. This suggested a seedling population of 350 seedlings 100m^{-2} at 8 years resulted from 1570 germinations, not unreasonable values.

Stand volumes (Table 27) were 33 to 50% of literature values (Table 31) for southern upland and poor sites, respectively. Both lower stand densities and smaller trees

Table 31. Literature reported stand volumes, dominant tree heights and stand densities for *P. mariana* sites (m^2 ha^{-1}, m and stems m^{-2})

Authors and vegetation type	Age	Vol. (m^3 ha^{-1})	Ht (m)	Density (stems ha^{-1})
Weetman and Harland 1964				
"Hypno-Picetum" Quebec	65	223.0	13.3	
Barney and van Cleve 1973				
Fairbanks, Alaska	51		9.4	21,079
	55		10.3	
Jameson 1964 *				
Northern Man.-Sask.				
black spruce/feathermoss	50	34.7	7.6	
	100	143.2	15.8	
	120	152.8	16.7	
black spruce/feathermoss	50	15.5	9.8	
	100	117.1	14.6	
	140	185.7	17.7	
black spruce/sphagnum	100	83.9	13.1	
	160	95.8	14.6	
black spruce/jackpine	140	108.5	15.3	
Moore and Verspoor 1973				
Northern Quebec				
"spruce-lichen woodland"				1,270
				3,080
"spruce-moss woodland"				4,840
				5,350
Horton and Lees 1961*				
Foothills, Alberta				
"Mesic upland"	50	128.7	10.6	
	100	268.0	16.8	
	150	309.3	19.3	
"Upland transition"	50	69.9	8.0	
	100	191.4	13.7	
	150	229.1	16.1	
"Shallow bog"	50	23.7	5.0	
	100	120.3	10.6	
	150	152.2	12.4	
Jeglum 1974				
Northern Ontario				
"Moist forest "			12.2	
"Picea/Ledum"			10.1	
			5.9	
"Muskeg"			4.6	
			1.5	

* Data taken from stand volume and height tables.

were responsible for reduced volumes. Densities were comparable to "spruce-lichen woodland" in northern Quebec (Moore and Verspoor 1973) and "Stereocaulon woodland" in the southern Northwest Territories (Kershaw and Rouse 1976) but were lower than southern populations (Horton and Lees 1961) and Alaska (Barney and van Cleve 1973). Dominant height growth also follows this pattern.

Seed production, in spite of reduced stand volumes and dominant height growth, was similar to reported values (Lebarron 1948, see Table 32), though no indication of stand age, growth rates or methods were given in the early study. Seed production in Lebarron's study was higher in the upland stand but further comparison would be tenuous. Initiation of seed production in Inuvik stands is delayed 15-20 years (Vincent 1965), which extends the critical interval for effective regeneration between fires and generally reduces

Table 32. Seed production of black spruce in Minnesota from Lebarron (1948) (seed $X10^5$ ha^{-1}).

New cones		1 Year-old cones	
Viable	total	Viable	Total
Swamp stands			
4.45	6.85	3.38	5.12
Upland stands			
16.21	21.90	8.22	11.11

seed production.

Quantity of seed produced, generally decreasing with stand volumes toward treeline, is greatly reduced in forest-tundra areas in response to the deformed nature of the trees (Fig. 47). These deformed trees never reach potential sizes or densities, hence the reduction in seed production.

Tree growth and seed production in Regions II, III, and IV is sufficient to regenerate stands at fire intervals between _ca_ 80 and 250 years but environmental effects on seed quality and germination may limit regeneration in Region II.

VII. VEGETATION

1. Methods

Vascular and cryptogamic plants were sampled at each of 19 sites with 25 rectangular, 20 X 50 cm (0.1 m^2) plots spaced at 1 m intervals along a transect (stands N, S, IIb, IIc and IIId used 10 X 20 cm plots, 0.02 m^2, for cryptogamic species). Cover was estimated by cover class and percent cover calculated from cover class mid-points. Frequency was calculated from presence-absence information for each plot and the data presented in an association table as percent cover and frequency. A "+" was used for cover values less than 1% and frequency values less than 10%. Species groupings were decided upon using cover and frequency differences. All P. mariana under 1 m in height were included in cover and frequency estimates, providing a measure of layering in older stands. Taxonomy followed Cody (1965) for vascular plants, Ahti et al. (1973) for lichens and Holmen and Scotter (1971) for mosses. Aulacomnium palustre includes A. acuminatum due to taxonomic confusion in the field and contrary to Ahti et al. the subgenus Cladinae is raised to full generic status as Cladina. Active layer depth was measured with a 1.2 cm diameter rod at 1 m intervals for 50 points.

2. Results

Burning of most of the *Picea mariana*/ *Vaccinium uliginosum*/ *Aulacomnium* spp. woodland occurred within the last 100 years, and stands spanning the range in ages from 8 to *ca* 300 years-old were sampled. No successional replacement of dominant vascular plants was found as most shrubs and herbs simply resprout after burning and soon achieve pre-burn prominence. On the contrary an orderly change of cryptogamic species was found suggesting a continuous succession. Four stages in this sequence were described based on growth related physiognomic changes and species changes with time since burning. All stages were found in Regions II, III and IV with only older stands (240+ years-old) sampled in Region I.

Stage 1, lasting from 1 to *ca* 15-20 years after fire (Fig. 43), was dominated by a mixture of the colonizing mosses *Ceratodon purpureus*, *Bryum psuedotriquetrum* and *Polytrichum juniperinum* (Table 33). The Lichen *Peltigera malacea* and liverwort *Marchantia polymorpha* also had high cover values with evidence of increased earlier cover of *Marchantia* found by excavation in 8 year-old stands. *Epilobium angustifolium* was the most conspicuous vascular plant with *Salix glauca*, *S. pulchra*, *Betula glandulosa*, *Arctagrostis latifolia* and *Calamagrostis canadensis* resprouting or quickly seeding back onto the site. Seedlings of *P. mariana* when present were generally obscured by the

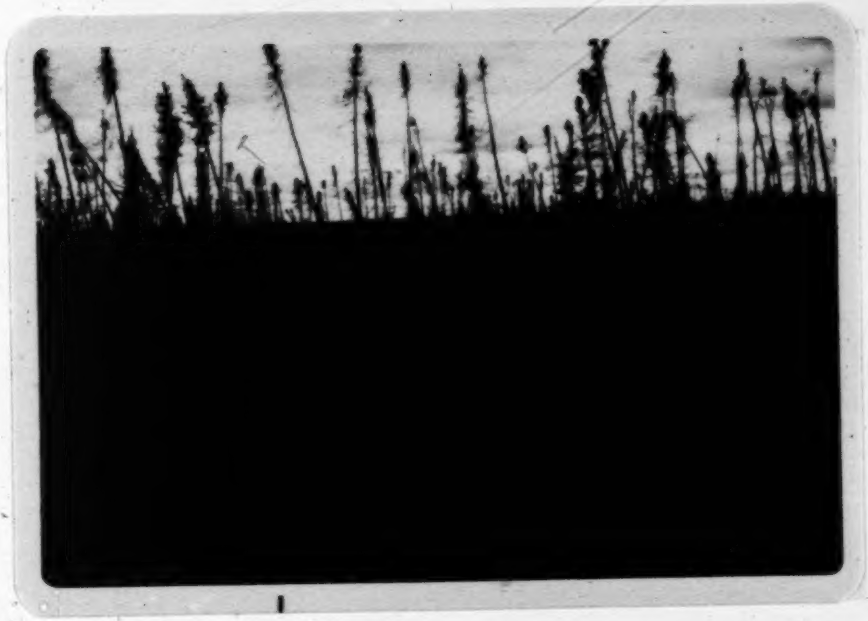

Figure 43. Stage 1 vegetation at Site S burned in 1968. Regrowth of Salix spp. is evident between fire killed trees. Picea mariana seedlings are ca 15cm tall after eight years.

Table 33. Association table with stands arranged in order of increasing age left to right. Diagnostic species for the four stages are boxed. Cover and frequency are separated by a ".".

	E	S	IIIh	IVa	IIc	IIe	IIb	IIId	IIIj	IVb
Picea mariana			10.48	19.40		11.44	6.+	12.20	+	
Moss cover	25.88	45.100	50.100	16.96	33.84	32.96	68.100	65.96	30.84	20.100
Lichen cover	+	7.92	11.68	12.96	30.92	8.92	4.76	4.48	29.96	20.88
Epilobium angustifolium	3.32	15.80	1.16					+		
Marchantia polymorpha	4.44	22.56								
Peltigera malacea	10.60	6.80								
Bryum pseudotriquetrum	3.56	2.92	+	4.75		+.35				
Ceratodon purpureus	63.96	39.92	+	11.45						
Polytrichum commune	+				+					
Polytrichum juniperinum	22.80	9.44	3.28	2.35	1.36		+		+	
Aulacomnium acuminatum	+.24	1.32	[illegible]	7.35	1.16	14.50	42.100	46.88	6.56	3.60
Aulacomnium turgidum	1.40	1.56	1.36	1.20	7.32	14.70	8.52	2.28	5.52	2.44
Vaccinium vitis-idaea	8.56	1.16	12.68	1.8	27.76	4.75	1.40	+	26.96	22.100
Vaccinium uliginosum	+	+	13.64	73.100	+	31.96	75.100	86.100	71.100	61.100
Cladonia spp.	+	+	1.32	25.56	6.84	6.24	+	2.32	5.56	11.60
Peltigera aphthosa			11.60	7.40		10.65	2.48	+	4.32	1.32
Peltigera canina			+				3.36	2.20	1.12	
Arctostaphylos rubra			3.12			+	8.64	1.+	2.20	2.24
Petasites frigidus			+				2.48	+.12		+
Saussurea angustifolia			+						2.24	2.32
Empetrum nigrum				+	1.16	+	1.12	2.+	6.32	
Hypnum revolutum						4.55	4.24			5.28
Hylocomium splendens				+		1.10	3.24	+	11.28	1.12
Cladina alpestris									+	+
Cladina mitis			+	+.25	20.76	1.10	+	+	20.76	6.32
Cladina rangiferina					+.20	1.+			+	+
Dicranum angustum	+			+	+	1.10	+	+	1.24	1.32
Dicranum undulatum		+			3.16	1.+	+		+	+
Dicranum elongatum				+	+		+		+	
Cetraria cucullata					+.16		+			+
Cetraria islandica					+					
Cetraria nivalis				+	+.16					+
Ledum palustre	9.48	+		+	14.96	+	+			+
Rubus chamaemorus	2.24			+	14.60					
Eriophorum vaginatum	6.24		+		13.28					
Sphagnum spp.	+			3.20	16.40	1.10				+
Spiraea Beauverdiana	1.24									
Alnus crispa		+								
Carex bigelowii		+				14.72				
Betula glandulosa	6.20		11.28	24.68	10.20	+.60	4.60	3.+	8.28	+
Ledum groenlandicum		4.20	5.24	19.76		2.56	7.68	5.52	12.80	4.48
Salix pulchra		4.36	49.84	20.72		+.12	+.12	+	+	8.36
Salix glauca	+	21.36	4.12	2.84		3.24	7.36	13.24	21.48	8.32
Equisetum arvense			6.76	+		+	2.68	+	+	+
Equisetum scirpoides		1.40	1.24			+	2.92	3.68	7.68	+.16
Calamagrostis canadensis	15.72	7.88	6.80				+.16	4.60	1.48	+.20
Arctagrostis latifolia		1.16	+.12			+.32	+	4.64	+	1.24
Rosa acicularis		3.24	+				+.16	2.36	1.32	
Ptilidium ciliare					+	1.10	+	2.+	+	
Tomenthypnum nitens			2.20	+	+	5.15	6.44	+	1.+	+
Pyrola asarifolia			+			1.36	+.16			+.12
Pyrola spp.			+.20	+		+	1.12			1.40
Liverwort	1.60			4.12		4.28	+			2.16
Brachythecium spp.			+	+.10		+.15		+	+	+
Drepanocladus spp.			+			+.20	+			
Drepanocladus revolvens			+				+	8.12		
Drepanocladus uncinatus			5.44			+.10		+	1.12	2.+
Eurhynchium pulchellum	—			+		+.15				
Graminoid	1.12			+		+				
Carex spp.			+		+			2.32		
Composite									+	
Lupinus arcticus							1.24			1.+
Betula occidentalis								+		
Pohlia nutans			+		+					
Stereocaulon spp.			+				+			
Peltigera horizontalis									+	
Pedicularis labradorica			+							
Astragalus alpinus	+	6.56		+						
Leptobryum pyriforme		+	3.16							
Oxycoccus microcarpus	+									
Peltigera spuria	+									
Pyrola secunda		+.10								
Ribes triste		+								
Ribes hudsonianum		+								
Hedysarum Mackenzii		+								
Chamaedaphne calyculata			24.68							
Shepherdia canadensis			4.12							
Parnassia palustris			+							
Alnus sp.						+				
Ditrichum flexicaule								+		
Dicranum muehlenbeckii										
Pleurozium schreberi										
Hypnum sp.										
Ranunculus lapponicus										
Andromeda polifolia										
Dicranum acutifolium										
Tetraplodon sp.										
Pedicularis sp.										
Dicranum groenlandicum										
Dryas integrifolia										
Stellaria sp.										
Rhododendron lapponicum										

Table 33 (continued)

	IIb	IIc	IIj	IIIe	IIIi	Ia	Ib	IIIa	IVc
Picea mariana			4.20	5.12	8.20	9.32	20.36	36.72	20.44
Moss cover	31.96	43.96	38.100	69.96	54.96	30.80	20.84	2.28	17.88
Lichen cover	11.84	12.80	39.92	49.96	12.76	41.84	65.96	94.100	71.100
Epilobium angustifolium									
Marchantia polymorpha									
Peltigera malacea									
Bryum pseudotriquetrum	+.15	+.20							
Ceratodon purpureus									
Polytrichum commune									
Polytrichum juniperinum	1.10	+.12						+	1.24
Aulacomnium acuminatum	1.10	2.24	12.56	5.48	1.24	+	+	+	+
Aulacomnium turgidum	21.60	5.60	12.52	3.28	1.20	+.12	2.40	+	1.16
Vaccinium vitis-idaea	46.100	22.100	32.96	39.100	55.100	18.96	21.100	12.88	39.100
Vaccinium uliginosum	12.52	+.16	27.88	44.100	14.56	7.64	16.64	+	+
Cladonia spp.	12.60	2.44	2.36	3.44	1.40	+	+	+.32	3.64
Peltigera aphthosa	2.10	+.12	3.48	5.40	2.24	1.24	+.12	+	1.16
Peltigera canina			+	1.20			+	+	+
Arctostaphylos rubra			+	10.64	3.32	3.16	2.+		
Petasites frigidus	10.64	+	+	+	1.+	+	2.40		2.32
Saussurea angustifolia				8.48	3.36				+
Empetrum nigrum	1.24		3.44	13.76	11.36	3.12	5.36	+	1.12
Hypnum revolutum	7.35	1.24			8.32	+	+		
Hylocomium splendens	3.20	+	4.36	4.24	12.48	8.40	6.36		+
Cladina alpestris			+	+	+	+	8.20	45.92	
Cladina mitis	8.30	12.84	33.80	39.88	5.40	10.48	21.84	[illegible].44	39.88
Cladina rangiferina	2.10	12.40	1.12	3.16	+	16.56	19.76	[illegible].84	19.48
Dicranum angustum	6.20	3.32	+	2.20	1.16	5.20	2.24		5.16
Dicranum undulatum	+	2.12	+	2.20	1.20	+	+	+	3.48
Dicranum elongatum			+	+	+	3.28	1.20		
Cetraria cucullata	+.15			3.12		4.44	1.12	+.12	+.12
Cetraria islandica	1.25					+.12	+.12	1.44	+.12
Cetraria nivalis	+	1.12		1.20		5.44	1.28	+.24	+.16
Ledum palustre	28.100	27.100	1.12		2.12	29.88	33.100	+	31.80
Rubus chamaemorus	5.32	1.32				5.28	+		+
Eriophorum vaginatum	+					5.36	4.12		
Sphagnum spp.	9.25	17.40				7.28	2.20		2.+
Spiraea Beauverdiana									
Alnus crispa	+	+				11.20	4.24		
Carex bigelowii						26.64	1.16		
Betula glandulosa	2.12	7.64	10.28			9.28	12.24		
Ledum groenlandicum	7.48	1.44	15.76	9.76	14.52	6.44	4.36	22.68	4.40
Salix pulchra	2.+		1.8		5.16	+	+	+	
Salix glauca	3.+	+	2.28	19.48	4.16	+	3.20	+	+
Equisetum arvense		+	+.20	1.16	+	1.32	5.80	1.+	
Equisetum scirpoides		+	+.36	2.72	1.32	1.+	5.88	+	
Calamagrostis canadensis	1.52		1.76	2.40			2.44	2.36	1.32
Arctagrostis latifolia	2.40	+	1.16	2.28	6.76	2.32	1.36	+	
Rosa acicularis	2.24		+	1.32	3.24				+
Ptilidium ciliare	2.+	1.+	+	3.32	15.56	+		2.24	1.+
Tomenthypnum nitens		+		2.12		1.32	3.28		
Pyrola asarifolia			+	+	11.60	11.60	1.+		
Pyrola spp.	+			3.56	1.24	2.36	3.44		
Liverwort		6.84	1.16	+			+		
Brachythecium spp.	+.15	+.16			+				
Drepanocladus spp.		+							
Drepanocladus revolvens									
Drepanocladus uncinatus									
Eurhynchium pulchellum	+.15								
Graminoid		1.32							
Carex spp.			+	+.16	+				
Composite							2.36		
Lupinus arcticus									
Betula occidentalis	+								
Pohlia nutans	+			+	+		+		
Stereocaulon spp.			+	+					
Peltigera horizontalis			+						
Pedicularis labradorica						+			
Astragalus alpinus		+							
Leptobryum pyriforme									
Oxycoccus microcarpus									
Peltigera spuria									
Pyrola secunda									
Ribes triste		+							
Ribes hudsonianum									
Hedysarum mackenzii									
Chamaedaphne calyculata									
Shepherdia canadensis									
Parnassia palustris									
Mnium sp.									
Ditrichum flexicaule									
Dicranum muehlenbeckii	+								
Pleurozium schreberi	3.+								
Hypnum sp.			+						
Ranunculus lapponicus			+						
Andromeda polifolia			+						
Dicranum acutifolium				+	+				
Tetraplodon sp.					+				
Pedicularis sp.						+			
Dicranum groenlandicum						+			
Dryas integrifolia						+			
Stellaria sp.							1.16		
Rhododendron lapponicum							+		

vegetation.

Stage 2, beginning 15-20 years after fire (Fig. 44), was dominated early by *Cladonia* spp. and *Peltigera aphthosa* with increasing amounts of *Aulocomnium palustre*, *A. turgidum*, *Hylocomium splendens* and *Peltigera canina* with age. *Vaccinium uliginosum* reached its highest cover and frequency (mean 54% and 83%, respectively) late in Stage 2 at 50-120 years (Table 33). *Petasites frigidus*, *Saussurea angustifolia* and *Empetrum nigrum* also increased in importance in southern stands. *P. mariana* penetrated the predominantly *Salix* canopy early in Stage 2 and was 2-3 m tall by 120 years old. Densities decreased in Stage 2 to a constant of *ca* 6,000 trees ha^{-1} and the active layer also decreased to an apparent constant (47.3 cm ±13.3SD, n=14) for all stands greater than 80 years-old.

Stage 3 vegetation, typical of stands 120 to 200 years-old, was found only in isolated forest stringers (Fig. 45), or around lakes and rivers in Regions II, III and IV. *Cladina mitis* and the mosses *Dicranum angustum* and *D. undulatum* became dominant with reductions in *Cladonia* and *Aulacomnium* species. Vascular plants generally decreased in cover apparently responding to increased canopy closure. Only *Vaccinium vitis-idaea* increased cover and frequency. Stand tree densities remained relatively constant as heights increased to 5-7 m.

Figure 44. Stage 2 vegetation at Site IIh. Complete cover of Vaccinium uliginosum is evident between ca 85 year old trees. The stake is one meter tall with ten centimeter bands.

Figure 45. Stage 3 vegetation at Site IIIe. Reduced shrub cover and increasing lichen cover are shown in this ca 185 year old stand. The stake is one meter tall with ten centimeter bands.

Stage 4, 200-300 years-old (Fig. 46), was the rarest stage, only found in four locations in Regions II, III and IV. Stage 4 *Picea mariana*/ *Vaccinium uliginosum*/ *Aulacomnium* spp. woodland was the only stage found in the pockets of forest in Region I (Fig. 47). *Cladina alpestris* (=*C. stellaris*), *C. mitis* and *C. rangiferina* increased cover and were the dominant lichens with *Cetraria cucullata*, *C. islandica* and *C. nivalis* present with high frequency but low cover. Most vascular plants were present only in reduced cover and frequency; only *Vaccinium vitis-idaea* maintained relatively high cover values.

P. mariana cover, indicative of layering, increased in stage IV and apparently responded to the death of canopy dominants. Total lichen cover also increased in Stage 4. Lichen cover generally increased with time since burning in all stages and was significantly correlated (r=0.8470, n=19) with age. Vegetation in general was homogeneous across treeline in *Picea mariana*/ *Vaccinium uliginosum*/ *Aulacomnium* spp. woodland with no measurable differences in species within and often between stages for most vascular plants. Only *Ledum palustre*, *Rubus chamaemorus* and *Eriophorum vaginatum* and mosses of the genus *Sphagnum* were found to increase cover and frequency in Regions I and II. *Cetraria* lichens were also more frequent in Regions I and II but these also increased in frequency in older stands (Stage 4) of Regions III and IV. Most Shrub species (i.e. *Salix glauca*

Figure 46. Stage 4 vegetation at Site IVc. Taller Picea mariana with butt-rot are breaking off. Increased layering is also present. The stake is one meter tall with ten centimeter bands.

Figure 47. Stand Ia showing deformed nature of *Picea mariana*. The stake is one meter with ten centimeter bands.

S. pulchra and *Ledum groenlandicum*) decreased in cover but were generally present in northern stands. Only *Alnus crispa* dramatically increased in Region I and may have been accidental in the stands sampled. *Betula glandulosa* was generally present but was a minor component of this woodland type. Other tree species (*Picea glauca*, *Betula resinifera* and *Larix laricina*) were occasionally present in sampled stands but were absent by 150-180 years after a burn. *Larix laricina*, a minor component (less than 1% of stems) of Regions III and IV stands, was not found in Regions I and II. Both *Picea glauca* and *Betula resinifera* were found in Regions II, III and IV but only *Picea glauca* was found in the forest-tundra, Region I.

C) Discussion

Cryptogamic recovery sequences (Fig. 48) after fire have been described for *P. mariana* woodland from other regions of the Northwest Territories (Maikawa and Kershaw 1976, Scotter 1964). These studies described early colonization stages to mature lichen woodland and in the Maikawa and Kershaw study lichen-woodland stages to "*Hylocomium-Pleurozium* forest". Scotter described a colonization stage of *Epilobium angustifolium*, *Marchantia polymorpha*, *Polytrichum spp.* and *Bryum psuedotriquetrum* similar to the present study whereas in the Maikawa and Kershaw study the colonization stage was dominated by

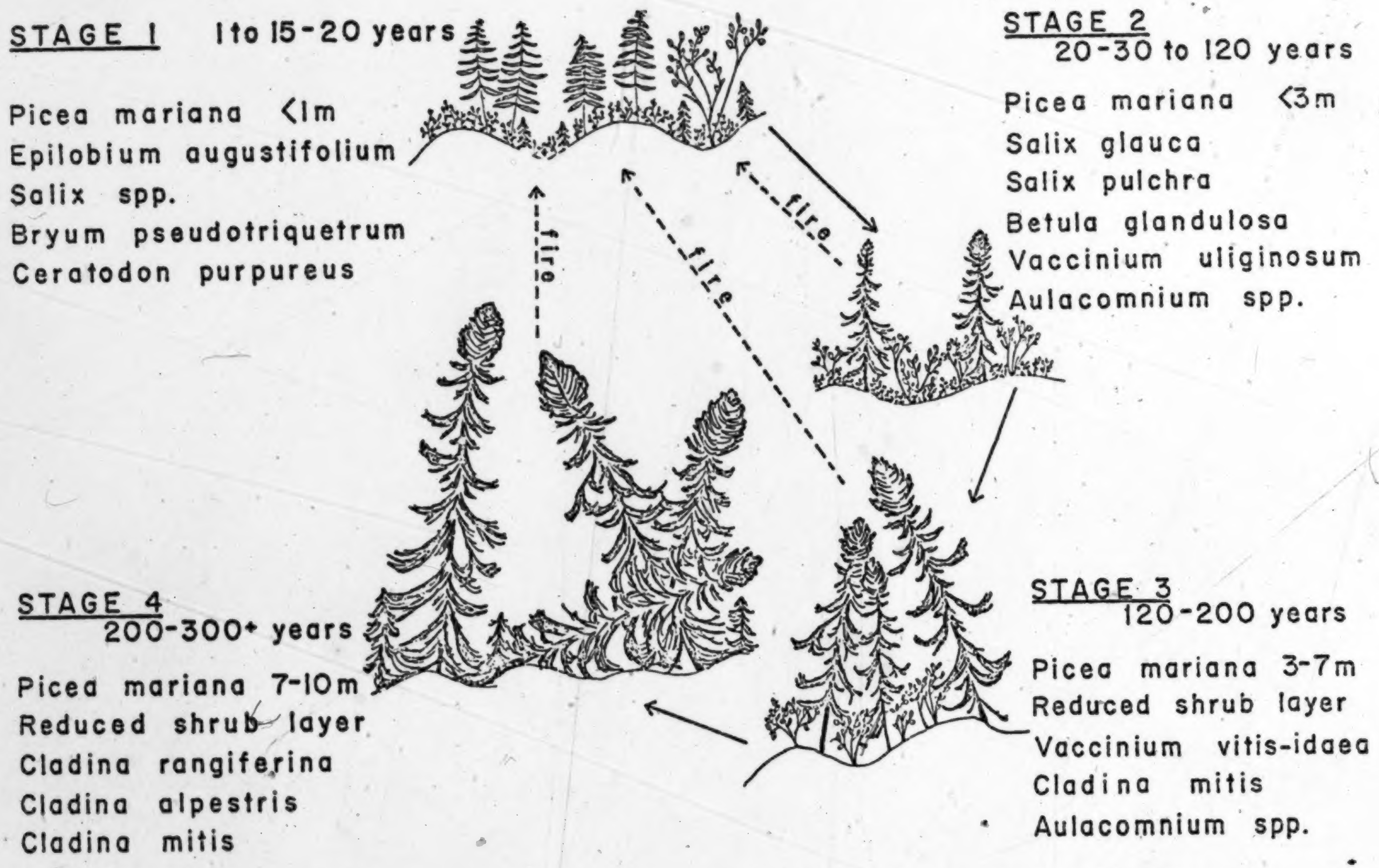
STAGE I 1 to 15-20 years
Picea mariana <1m
Epilobium augustifolium
Salix spp.
Bryum pseudotriquetrum
Ceratodon purpureus
STAGE 2
20-30 to 120 years
Picea mariana <3m
Salix glauca
Salix pulchra
Betula glandulosa
Vaccinium uliginosum
Aulacomnium spp.
fire
fire
fire
STAGE 3
120-200 years
Picea mariana 3-7m
Reduced shrub layer
Vaccinium vitis-idaea
Cladina mitis
Aulacomnium spp.
STAGE 4
200-300+ years
Picea mariana 7-10m
Reduced shrub layer
Cladina rangiferina
Cladina alpestris
Cladina mitis

Figure 48. Diagrammatic representation of the vegetational sequence with fire.

Polytrichum piliferum and Lecidea spp. Both studies report invasion of Cladonia spp. and Cladina spp within 20-25 years and domination of the ground cover by Cladina spp. and Stereocaulon spp. (Stereocaulon paschale in Maikawa and Kershaw 1976) between 50-60 and 120+ years. This invasion and dominance of the ground cover by lichens was found to be 60-100 years sooner than in the Picea mariana/ Vaccinium uliginosum/ Aulacomnium spp. woodland in the lower Mackenzie Valley. The delay found was apparently caused by the increased and prolonged dominance by shrubs (i.e. Vaccinium uliginosum, Salix glauca, S. pulchra and Betula glandulosa) not present in the reported southeastern studies. The most plausible explanation for this phenomenon is the different substrates, coarse sandy soils for both comparative studies (Maikawa and Kershaw 1976, Scotter 1964) and fine textured tills in the present study. The latter leads to improved water and nutrient availability and more luxuriant plant growth.

The described early colonizing stage (Stage 1) was found south and east in the Lower Mackenzie Valley by Reid (1974) and Zoltai (1975b) confirming the widespread distribution of this stage. Reid reported a similar "open black spruce/Ledum/Cladonia" (Ledum groenlandicum) vegetation type between Fort Good Hope and Fort Norman in the southern limit of the Lower Mackenzie Region. Reid however does not report the existence of tall shrubs (Salix glauca, S. pulchra and Betula glandulosa) suggesting the tundra affiliation of the vegetation in the present study.

The presence of Ledum palustre in most stands of Regions III and IV and its dominance of stands in Regions I and II was found similar to reports by Larsen (1965, 1971a) from east of Great Slave Lake and 500 km southeast of Great Slave Lake. Larsen's studies also only found Betula glandulosa present in northern stands though no mention of Salix glauca and S. pulchra was made.

The existence of Picea mariana/ Vaccinium uliginosum/ Aulacomnium spp. woodland appears restricted to the lower Mackenzie Valley (Region B.23b, Rowe 1972). In other open boreal forest studies (Hustich 1957, Ritchie 1959, Scotter 1964) the ubiquitous shrub Vaccinium uliginosum has been reported but not the persistent shrub and moss dominated stage, characteristic of these more northern woodlands.

VIII. SIMULATION MODEL

A) Model structure

A stand reproduction model of P. mariana was constructed with empirically derived field information using a discrete event formalism. Wildfire destruction of a stand was the "event" upon which the model calculations were based. Each iteration of the model therefore consisted of the post-fire stand regeneration calculated from the reproductive potential of the preburn stand.

Driving variables for the model were degree days, mean return interval of wildfire and standard deviation of the return interval. Degree days provided the environmental input for all growth, seed quality and germination calculations. Mean return interval provided the time element for all growth and competitive interaction with standard deviation of the return interval facilitating the introduction of variability to the model. Normally distributed return intervals may not be the most appropriate statistical distribution for burn intervals (Rowe et al. 1975), but were nevertheless used out of practical considerations. Exponential or Weibul distributions of the return interval of fire would be possible alternative distributions.

The state variable stand density was returned from each iteration, as established 1 year-old seedlings and the modelling unit was one 10x10 m plot (0.01 ha). The model is programed in APL (Appendix I) and an abreviated flow diagram is presented in Fig. 49.

The model was initialized with a density of 40 trees 100 m^{-2} and given desired degree day, return interval and standard deviation values. Specifying the duration of the run (time in years) started the model.

Using return interval and standard deviation, a normally distributed random number generator determined the burned stand age. This age was used to determine competitive reductions of stand density to average field densities (Equation 6). Average stand density described by a third order polynomial was used instead of the possible power function model of mortality (Equation 4, pg. 101) thereby simulating density increases in old age stands (Fig. 38). Densities above average were reduced to average and densities below were allowed to remain below average simulating competitive thinning of the trees.

Mean tree size (volume) in the stand was calculated from a multiple regression function (see Table 26) of degree day, density and age values generated previously by the model. The size of each pre-burn stand tree was then generated by calling for normally distributed random numbers with mean as the mean tree size, standard deviation which

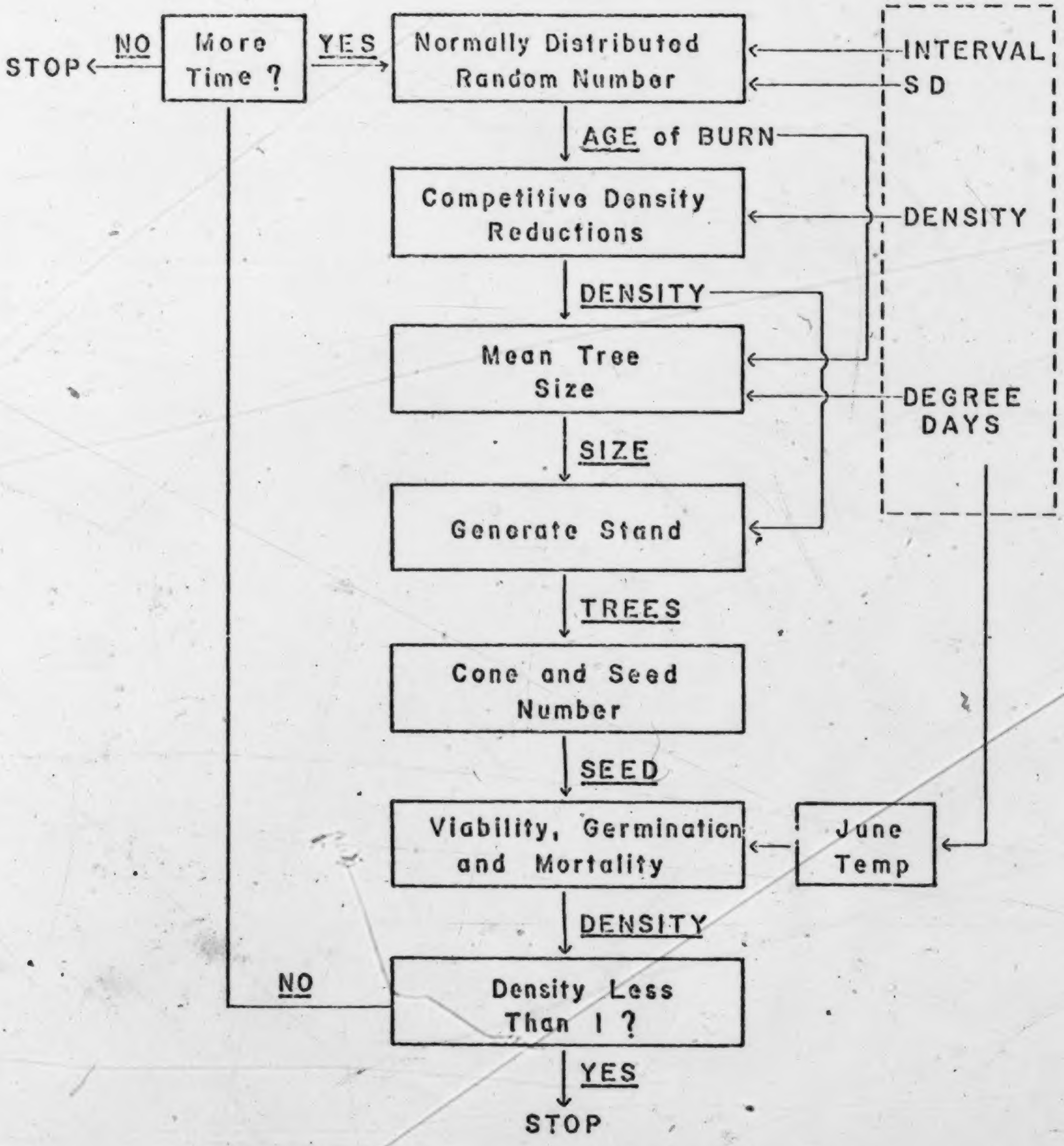
STOP
NO
More Time ?
YES
Normally Distributed Random Number
INTERVAL
SD
AGE of BURN
Competitive Density Reductions
DENSITY
DENSITY
Mean Tree Size
DEGREE DAYS
SIZE
Generate Stand
TREES
Cone and Seed Number
SEED
Viability, Germination and Mortality
June Temp
DENSITY
NO
Density Less Than 1 ?
YES
STOP

Figure 49. Flow diagram for simulation model. Boxes indicate calculations. Underlined names are calculated variables. Dashed box surrounds driving variables.

can be calculated from the mean tree size (Equation 7) and number of size values equal to density.

Cone, and ultimately seed number, were calculated for the simulated stand by determining the number of cones per tree (Equation 8), multiplied by the average seed per cone (73) and summed by plot. The underlying assumption is that all seed produced are released and no predation reductions occurred.

Calculation of post-burn established seedlings began with germination potential of the seed determined by the relationship:

$$Q=-140.39+58.19J-8.15J^2+0.3892J^3 \qquad (10)$$

where J is the June mean temperature of the previous year and Q the percent germination of the seed population. This was a best fit relationship (Fig. 50) tc the environmentally reduced germination potentials found in the 1975 cone crop (see germination section). June mean temperature was described as (Fig. 51) linearly related to degree days (r=0.9053, n=16) by:

$$J=-4.98+0.01204D \qquad (11)$$

where J is June mean temperature and D the degree day driving variable. Potential germinating seed was germinated by the relationship:

$$G=-22.8+2.60J \qquad (12)$$

where G is the percent germination and J is June mean temperature (Fig. 34). Germination was first reduced by 33%

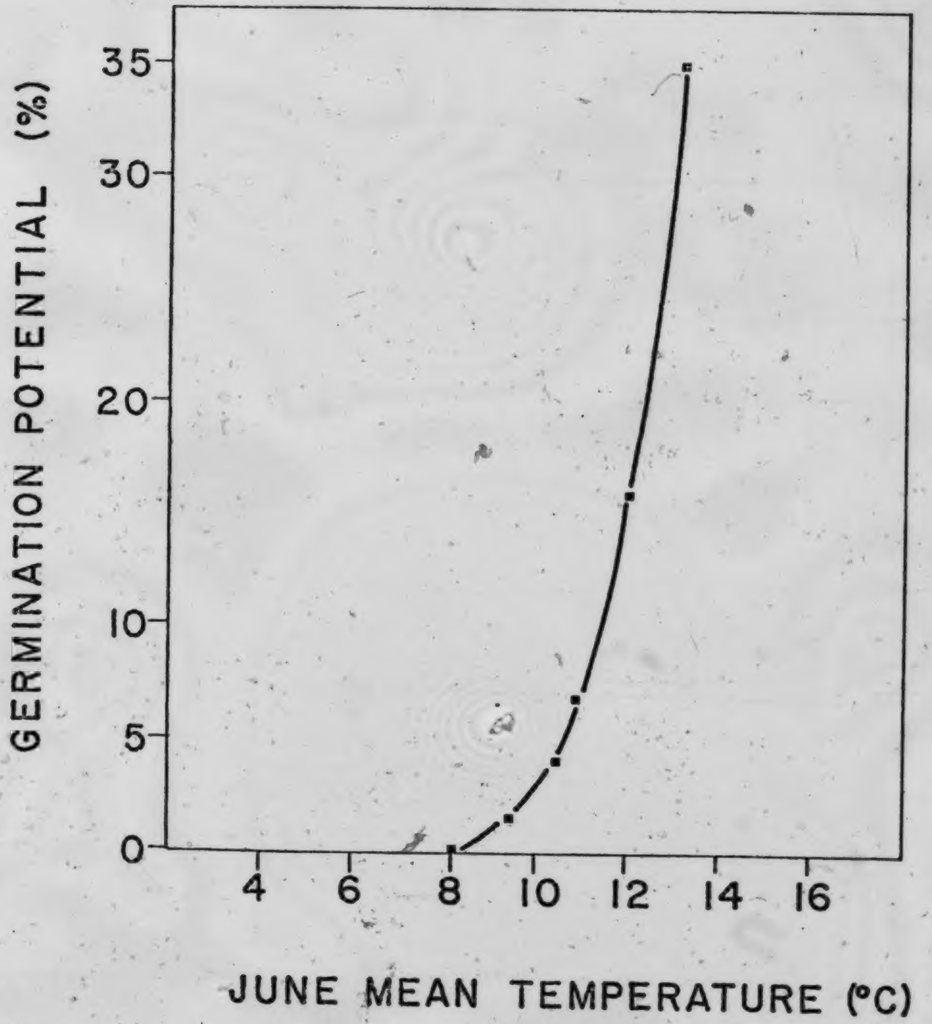

Figure 50. Seed germination potential as a function of the previous year June mean temperature. The line is a least squares polynomial curve fit.

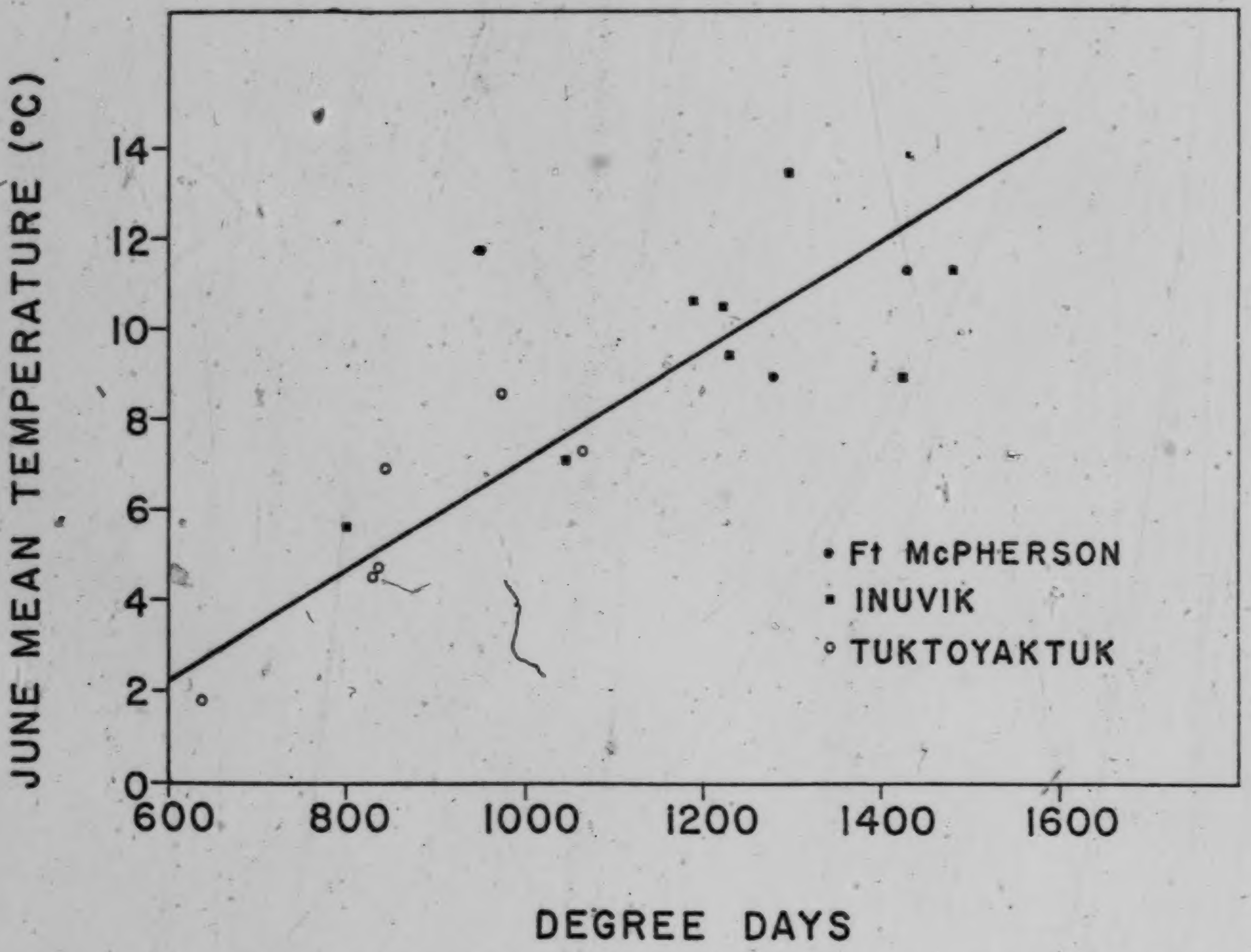

Figure 51. June mean temperature as a function of degree days. The line is a linear regression of the data.

for the restriction to hummock side and trough microsites, assuming even seed rain into all microsites. A first year mortality constant of 0.44 was then applied resulting in established 1 year-old seedlings returned as the state variable density for the next iteration. Densities less than 1 were returned as 0 and the run was terminated.

Burn ages were summed from each iteration and runs terminated when summed burn ages exceeded the total requested time. All test runs were a minimum of 10 iterations and data points were density means of the last 5 iterations.

B) Testing and Results

Reduced reproduction, as would be expected in forest tundra regions, was defined as less than 950 1 year-old established seedlings 100 m^{-2}. This value was determined from the power function model (Equation 4) as the number of 1 year-old established seedlings required to maintain average densities throughout the stand "lifetime". Therefore open boreal forest was defined for the model as reproduction greater than 950 1 year-old seedlings, forest-tundra as 1 to 950 seedlings and tundra as no reproduction.

Application of these criteria to simulation data (Fig. 52) predicted treeline and forest line to be ca 40 km south of the current position for 100 to 225 year burn

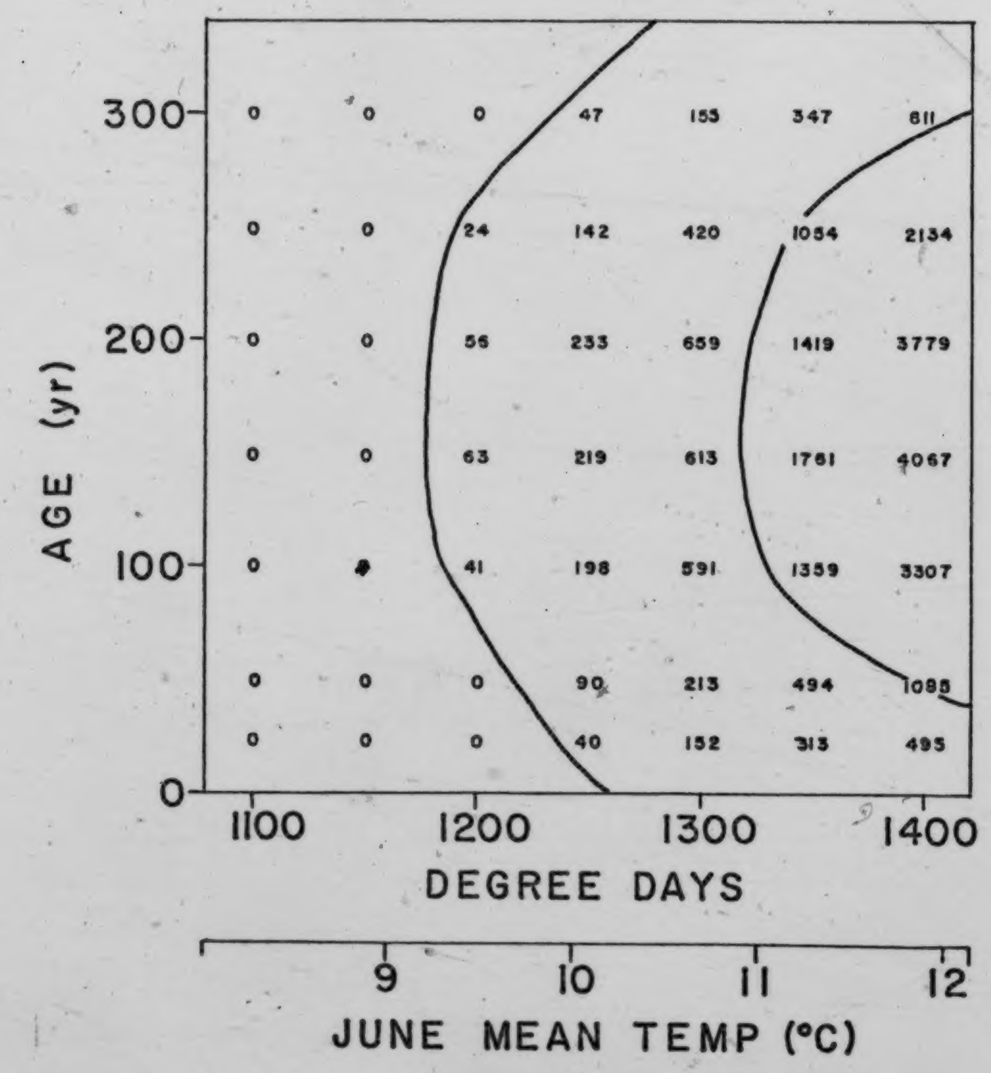

Figure 52. Model predicted seedling establishment at differing ages and degree day values. Solid lines separate simulated tundra, forest-tundra, and open boreal forest, left to right.

intervals. Burn intervals less than 100 years were generally encountered along the study transect, therefore the 40 km treeline and forest displacement would be conservative. Simulated burn intervals less than 100 years caused further retreat of treeline and particularly forest line. Short return intervals were observed in the field to limit reproduction. For example, a 19 year burn in Region III (near Sites IIIi and IIIh) and 20-40 year return intervals in Region II (near Site IIe) both resulted in elimination of _P. mariana_. Simulated and field reproduction appeared to be limited by seed production in these age classes.

Simulated burn intervals between 100 and 225 years resulted in no reduction in reproduction (Fig. 53), inferring ample seed for stand regeneration. Simulated stand ages and burn intervals greater than 225 years showed a marked decrease in reproductive potential associated with senescence of the stand. Field observations supported this reduction with the observed mortality of old individuals and increased layering in stands 250+ years old. Increased layering would increase density but not immediately add to the seed reproduction potential lost with the canopy dominants.

The ultimate control, however, in simulated reproduction appeared to be temperature control of seed germination. Tests of the simulated environmental reproduction limit showed direct correspondence of the X

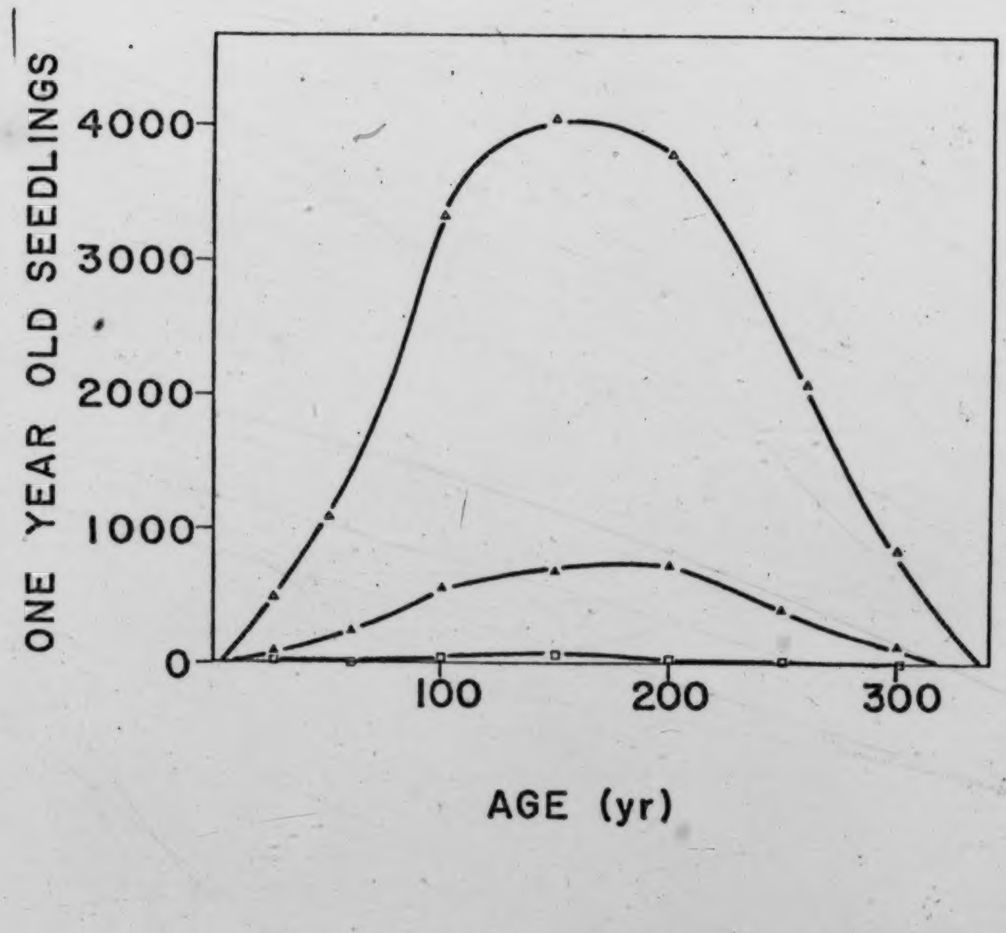

Figure 53. Simulated reproduction of Picea mariana showing plateau at 100 to 225 years (□=1200 degree day simulation; ▲=1300 degree day simulation; △=1400 degree day simulation).

intercepts and sample means between the germination vs. June temperature function and 80% confidence limit equations of the regression coefficient and the simulated results (compare Figures 54 and 34). Confidence limits of 80% were used due to the inverted nature of 95 and 90% confidence limits of the slope. Shifting the germination temperature relationship to the 80% confidence limits moved simulated tundra and forest-tundra ecotone ca 60 km (Fig. 55 and 56) suggesting the importance of this limitaion to *P. mariana* reproduction. Temperature relationships also affected simulated reproduction at the forest-tundra and open boreal forest ecotone and moved this boundry ca 10-20 km. Simulated temperature reduced germination should have moved this boundary ca 80 km suggesting other controlling factors. The simulated open boreal forest and forest-tundra ecotone occurred near the point at which reproduction became exponential (Fig. 57). The exponential function of cone number to tree size (Equation 8) and increasing growth rates may account for this observation and explain the change in controlling factors.

C) Discussion

Empirically derived forest models generally are of two types, forest production models (Opie 1968) and forest population and succession models (Leak 1970, Botkin et al. 1972, Shugart et al. 1972). Forest population

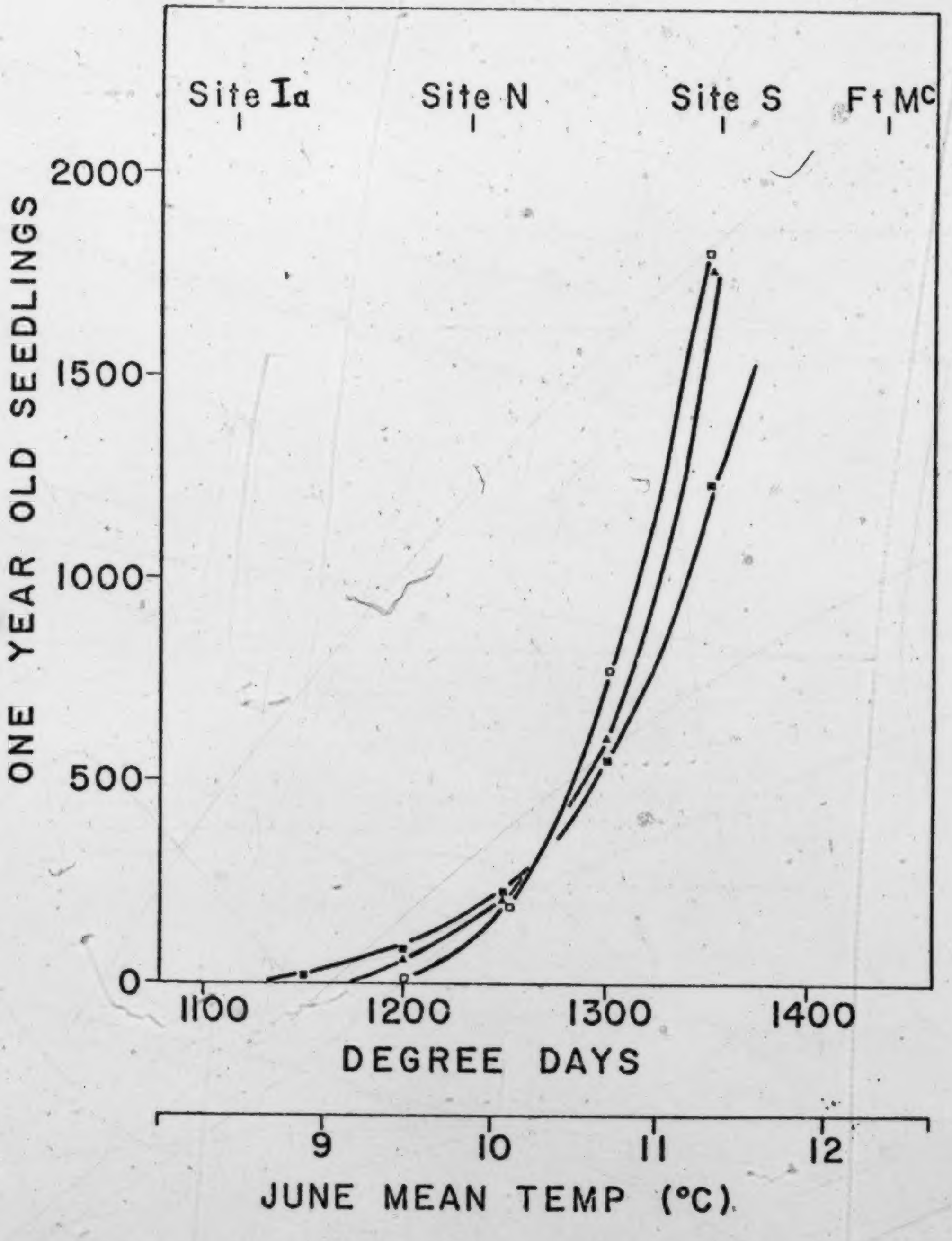

Figure 54. Simulation results of varying the germination relationship (▲=model June mean germination relationship; □ =upper 80% confidence limit of slope; ■=lower 80% confidence limit of slope) .

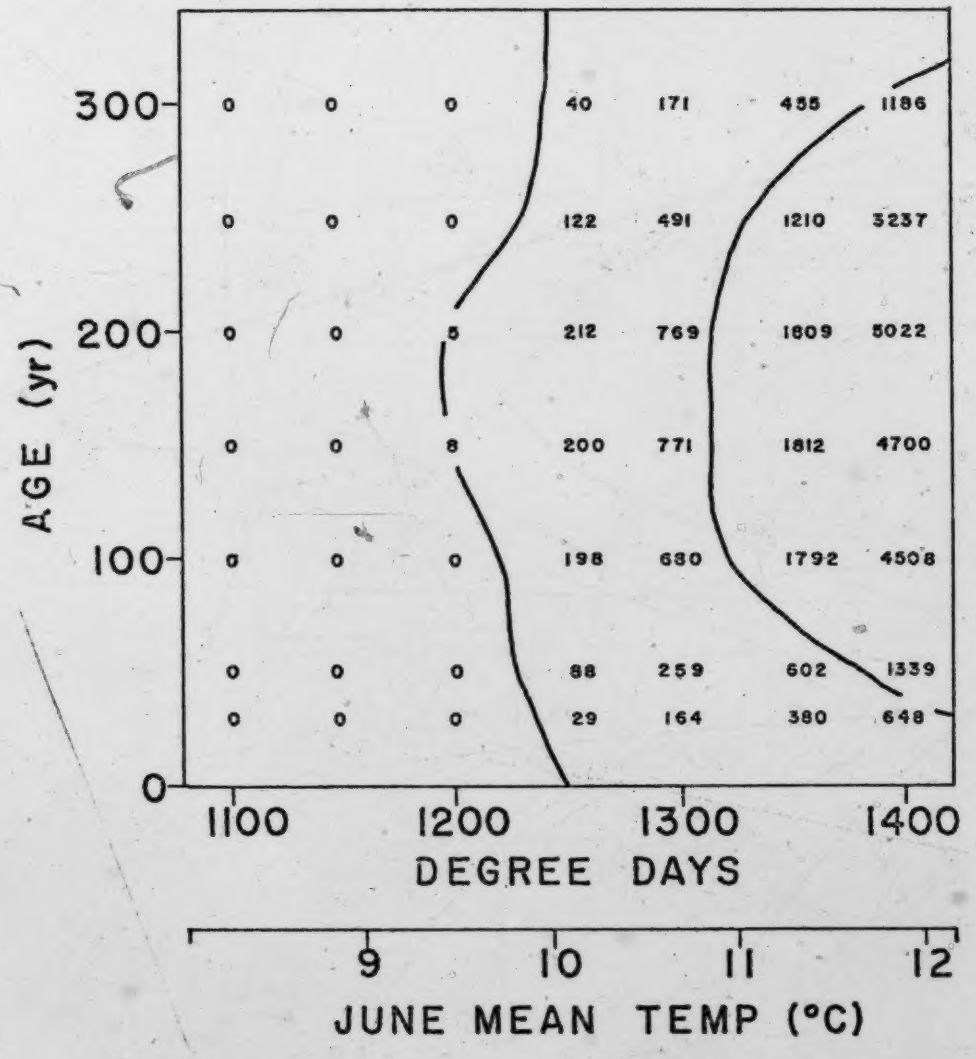

Figure 55. Upper 80% confidence limit of the germination and environment slope and resultant establishment. Lines separate tundra, forest-tundra and open boreal forest.

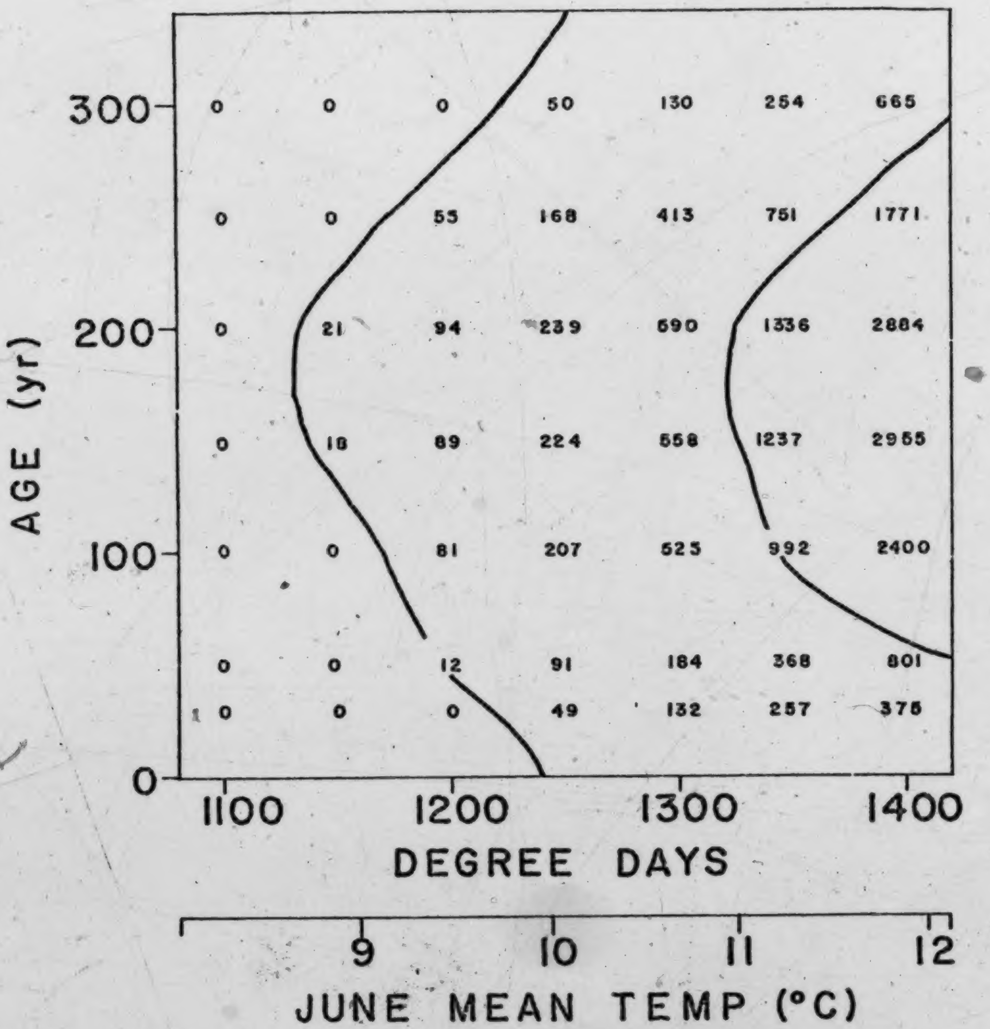

Figure 56. Lower 80% confidence limit of the germination and environment slope and resultant establishment. Lines separate tundra, forest-tundra and open boreal forest.

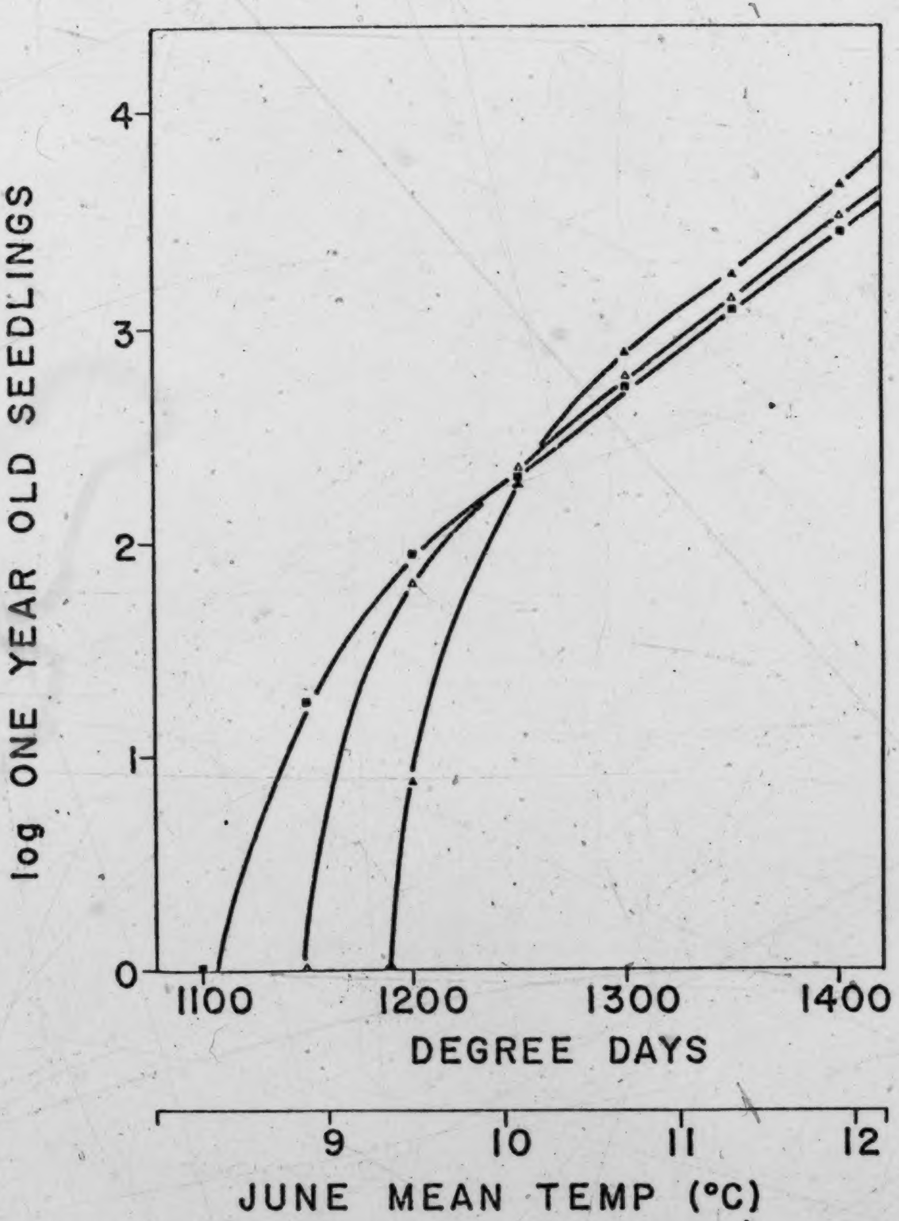

Figure 57. Log plot of simulated establishment and 80% confidence limits of germination and environment slope (△=model results; ▲=upper 80% confidence limits; ■=lower 80% confidence limits).

modelling had its beginning with models based on survivorship probabilities of mixed species stands (Leak 1970). Leak's model assumed any of the modelled species were able to enter the stand, then subsequently remain in the stand independent of environmental and competitive factors. Botkin et al. (1972) elaborated on this model by introducing environmental and competitive control of growth and reproduction but assumed all species capable of dispersing an equal number of disseminules to the site. These earlier models did not attempt to model seed production or environmental effects on reproductive success.

The present model is an attempt to introduce species reproduction into the modelling effort and also the use of an approach centered upon a single event in the system. This discrete event approach has been successful in demonstrating the importance of germination limitations and secondarily seed germination potential to stand success. This suggests the necessity of incorporating reproduction modelling into forest simulations.

Limitations imposed by environmental reductions in seed germination provided the control of reproduction for the relatively constant "environment" of the model. When placed in perspective with field environmental variability, this germination limit would provide the mechanism for rapid but local (within a burn) removal of P. mariana south of predicted boundaries by adverse but short term weather conditions. Long term climatic change would, however, first reduce the reproductive potential through reduced tree growth, reduced cone and seed production and could probably act to reduce germination potential in the first 6-8 years. This could conceivably result from a 2°C change in June mean temperature (if the correlation is valid, Fig. 50), the result of only an 80-100 km shift in weather patterns.

Fire interval affected the simulation only under extreme circumstances, for example extremely long (225+ years) or short (<80 year) intervals. Both of these effects were apparently the result of reduced seed production by young and old senescent stands. Suggested by this was the importance of burning in stand maintenance and the importance of timing of the burn for effective reproduction. Long term attempts at fire exclusion could therefore ultimately have similar results as repeated burns of short interval.

In conclusion, the model provided a consistent mathematical examination of the field information and aided in the identification of potential inconsistencies. The result was a presentation of information concerning treeline and possible results of potential changes both man made and natural. Improvements to the model could be made with a better understanding of: 1) burn intervals and distributions; 2) data concerning seed production vs. seed release after fire; 3) the fate of released seed; and 4) microsite distribution related to region and burn intensity.

IX. GENERAL DISCUSSION

The climatic gradient and fire interval near treeline interact in controlling the success of *Picea mariana* in the lower Mackenzie Valley. Changing along this gradient are daily mean summer temperatures, length of the growing season and annual precipitation. Climatic control of the reproductive stages is primary in the life cycle. Low temperature and a short growing season set the limits of seed germination potential and seed germination. In contrast, mature trees are capable of vegetative growth and reproduction in environments not conducive to sexual reproduction.

Limits to vegetative growth of *P. mariana* may result from mechanical damage by wind abrasion or water stress, the result of anatomically immature needles (Baig and Tranquillini 1976). These growth limiting factors probably act only in the forest-tundra region and certainly are not evident south of forest line. Long term growth reduction may, however, directly limit cone and seed production as shown in reduced seed size and germination potential in the forest-tundra. Seed germination potential is reduced south of the forest line compared to southern populations, suggesting unfavorable carbon balance or limited development due to the short growing season. Germination potential is relatively constant from forest line south (Regions II, III and IV), suggesting little plant response to an almost 3°C differing daily mean temperature. Reduction of temperature similar to the forest-tundra region could however eliminate production of potential germinating seed. Such limitation over 5 to 10 years would exhaust the retained seed reservoir. Temperature reduced seed germination, through the 15°C lower cardinal limit, is probably the ultimate control of P. mariana at treeline and successful stand reproduction south of forest line. The relatively short period of time (1-6 years) possible for establishment after a fire accentuates the precarious nature of treeline. This short period for effective establishment is due to seed longevity in cones and apparent destruction of ungerminated seed in the soil. Together the lower cardinal temperature for seed germination and limited establishment time make possible the rapid retreat of treeline reported by Nichols (1975). Short term, 1 to 10 year, changes in climate could therefore result in large areal changes in vegetation near forest line in view of the size of recent wildfires in the study area. Major changes in tree cover over large areas may therefore not reflect more than minor and only short term changes in climate near the forest line. The 50 year recovery time for forests after fire reported by Nichols (1975) should be reinterpreted in context with the limited establishment time available for P. mariana after fire. The apparent 50 year recovery period probably is the result of the required time before detectable amounts of pollen are produced and recorded in the pollen record. Actually Picea is present throughout this time period.

Climatic reconstruction should be possible based on the climatic requirements for reproduction of _P. mariana_. Estimated minimum average temperatures for "reliable" reproduction of _P. mariana_ in the District of Mackenzie are 11, 14 and 11°C for June, July and August, respectively. These are temperatures estimated from _ca_ 40 km south of modern forest line. Temperatures of 9.5, 13 and 10°C are minimum estimates below which no successful establishment would be expected. Degree days of 1200 and 1330 are estimated limits for no establishment and reliable establishment, respectively. These values provide a basis for climatic reconstruction if caution concerning environmental variability is incorporated.

Ritchie and Hare's (1971) 5°C and Nichol's (1976) 4±1°C estimated increases in mean daily summer (June, July and August) temperatures for ecotonal movements on the Tuktoyaktuk peninsula are _ca_ 1°C higher than the estimated temperatures for reliable reproduction. This assumes these estimates were based on Tuktoyaktuk and Ennadai Lake, June, July and August mean temperatures (4.4, 10.6 and 8.9; 6.7, 12.8 and 11.7°C; respectively). Further, in support of these increases above required temperatures, was Ritchie and Hare's observation of greater radial increments on a fossil stump from the late-Hypsithermal (4,940±140 radiocarbon years B.P.), than increments from near modern forest line.

Vegetational changes across treeline reflected increasing tundra influences south to north. The vegetational change, with increased number of tundra species, adjacent to forest line may result from oscillations of treeline and be historical in origin rather than in equilibrium with modern climate. Most of the stands adjacent to forest line are pre-1850 in origin and probably reflect earlier warming during the 18th and 19th centuries referred to by Nichols (1976). In general, understory species are gradually reduced in cover and size across treeline south to north with only the forest cover providing a visible change.

Neaf the forest line the hummock and hollow sequence directly influenced establishment by restricting germination to _ca_ 66% of the terrain surface, the side and trough microsites. Hummock development increases both in development and occurrence, south to north (Zoltai and Tarnocai 1974) and may further restrict establishment in northern areas. Hummock topography may differentially affect seedling growth rates and success. No evidence was found of aspect related tree distribution in the hummock sequence though, this may be explained by the continuous insolation during the germinating period. Differential growth rates are probable in the hummocky terrain and may become important in determining tree growth and ultimately mortality of suppressed trees. Interference and death of such trees even in open boreal forest would be expected in smaller weakened individuals as with other plants (White and Harper 1970). These possible microenvironmentally induced differential growth rates would also explain errors associated with stand ageing techniques.

Germling to 1 year-old seedling survivorship was not affected by microsite but indications were that future seedling mortality may change. Little or no increase in seedling growth was observed in some plots especially trough microsites and regrowth of Polytrichum spp. had overtopped many seedlings by the end of the second year. No grazing damage of P. mariana seedlings was observed, this however does not preclude future reduction of seedling numbers by this mechanism.

Management of open boreal forest should reflect the plasticity of this dominant tree species. As suggested by the model presented earlier, fire interval is unimportant to reproduction as long as it is ca 80 to 225 years due to seed retention in cones and constant tree densities. What this statement did not say is that burning must occur for stand regeneration by seed. The semi-serotinous cones of P. mariana (Vincent 1965) and small seed size require burning to open the cones and to remove accumulated duff and interfering vegetation for effective establishment. Fire suppression prevents this necessary environmental change and may reduce reproductive potential of a stand in extreme situations (225+ years). Cyclic burning and regeneration were found to be important (Kershaw 1977) for the maintainence of lichen woodland and caribou winter range in the District of Keewatin. This successional sequence described by Kershaw to closed spruce "Hylocomium-Pleurosium forest" within 200 years would probably not apply to the lower Mackenzie Valley, where observed changes in understory sequences culminate in pure lichen carpets in the time period. These pure lichen carpets are associated with senescence of *P. mariana* but may actually increase the quality of caribou winter range.

Important also to the management of open boreal forest is the revegetation of damaged surfaces (i.e. seismic lines, borrow pits and construction and gas well sites). Revegetation by direct seeding of *P. mariana* would be quite risky due to unpredictable seasonal variation in climate at the northern limit of the species. Improved success might be obtained by light burning of the surface or scarifying and sowing seed onto snow or immediately after spring snow melt. No germination of seed should be expected the second year after seeding due to apparent destruction of seed in the soil.

In general direct seeding of cut lines or seismic lines would yield minimal results. These areas would be best left for natural seeding providing there is a nearby seed source. Vincent (1965) reported seed dispersal dropped to zero only ca 100 m from a stand edge. This provides an estimate of the maximum area for natural seeding of P. mariana but does not consider dispersal onto snow surfaces. Planting seedlings would increase success rates. Transplanted experimental seedlings into any microsite were found to be 100% successful. This would however be a labor intensive operation on an intact peat mat.

In spite of these restrictions, why does P. mariana remain most successful at forest line in the Lower Mackenzie Valley? The answer probably lies in the adaptation to burn cycles and tolerance of cold wet soils. P. mariana maintains a relatively constant seed population which is little affected by the burn interval, is not destroyed by fire and accumulates on the tree over a period of years. Larix laricina and Picea glauca on the contrary release seed annually, maintaining no such seed population and therefore must seed from survivors over longer distances. The continuous nature of the forests on the flat till plains results in large burned areas and few survivors, which limits and localizes the potential seed dispersal of P. glauca and L. laricina. Picea mariana in contrast floods the burned site with seed stored in cones of previous years immediately after fire, capitalizing on the reduction in interfering vegetation and improved soil thermal regime (Rouse and Kershaw 1971).

In the absense of burning, a rare occurrence south of forest line, layering of _P. mariana_ serves to maintain the species on a site with little evidence of replacement. Mixed tree stands of _Picea glauca_, _Larix laricina_ and _P. mariana_ mature to purely _P. mariana_ dominated stands. Site alteration by peat accumulation and permafrost aggradation restricts root systems to surface horizons. This results in severe growth restriction and stand thinning. Stand thinning is generally at the expense of _Picea glauca_ and _Larix laricina_. _Larix_, though faster growing than _P. mariana_ appears to be shorter lived (150-180 years, maximum), especially in mixed stands. Therefore the reproductive alternatives open to _P. mariana_ make it persistent in burn cycles of almost any interval and results in its dominance as a treeline species in boreal North America.

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APPENDIX I

APL program of the model. The first function is the main command program and all other functions are subroutines of it.

```
  ∇MODEL[⎕]∇
  ∇ R←MODEL TIME;DEN;TOTAL;AGE;SIZE;TREES;SEED
  DEN←DENSITY
  JUNE←¯4.98+DEGREE×0.01204
  TOTAL←0
 L1:AGE←SD RANDN INTERVAL
  DEN←AGE COMPETITION DEN
  SIZE←AGE VOLUME DEN
  TREES←DEN STAND SIZE
  SEED←CONE TREES
  DEN←SEED GERM JUNE
  →(DEN>0.5)/L2
  DEN←0
 L2:TOTAL←TOTAL+⌈AGE
  'AGE OF BURN WAS  ' ,(⍕⌈AGE), ' YEARS    DENSITY IS NO
  W  ' ,(⍕DEN), '  TREES/100M2     TOTAL TIME IS  ' ,(⍕
  TOTAL), '  YEARS'
  →(TOTAL>TIME)/0
  →(DEN>0)/L1
  'BURNING HAS ELIMINATED TREES FROM THE SITE'
  →0
  ∇
```

```
  ∇RANDN[⎕]∇
  ∇ R←SD RANDN MEAN;INDEX
  →(1<⍴MEAN)/L3
  R←MEAN+SD×¯6+(+/¯1+?12⍴178956970)÷178956969
  →0
 L3:R←INDEX←0
 L1:INDEX←INDEX+1
  R←R,MEAN[INDEX]+SD×¯6+(+/¯1+?12⍴178956970)÷178956969
  →(INDEX=⍴MEAN)/L2
  →L1
 L2:R←R[1+⍳(¯1+⍴R)]
  →0
  ∇
 ∇COMPETITION[⎕]∇
 ∇ R←X COMPETITION Y
 R←⌈346.039+(¯4.78975×X)+(0.023512×X*2)+(-0.0000356527×
 X*3)
 →(Y≤R)/L1
 'COMPETITION IS CONTROLLING DENSITY AT  ' ,(⍕R), '  TR
 EES PER 100 M2'
 →0
L1:R←Y
 →0
 ∇
```

```
 ∇VOLUME[⎕]∇
 ∇ R←X VOLUME Y;LAT
 →(1356≤DEGREE)/L1
 LAT←71.98183+DEGREE×¯0.002924
 →L2
L1:LAT←78.697522+DEGREE×¯0.007877
L2:R←90.18977+(LAT×¯1.33455)+(¯0.0085306×Y)+(X×0.021626
 )+(¯0.000065758×X*2)
 R←10*R
 ∇
```

```
 ∇STAND[⎕]∇
 ∇ R←X STAND Y;S
 R←Y×((R←⍳X)>0)
 →(Y≥2.4)/L1
 S←0.106+2.09×Y
 →L2
L1:S←3.0436+0.8032×Y
L2:R←S RANDN R
 R←(R>0)/R
 →0
 ∇
```

```
 ∇CONE[⎕]∇
 ∇ R←CONE X
 X←X×1000
 R←¯1.1393+0.6498×(10⍟X)
 R←+/((10*R)>0)/((10*R)×73)
 ∇
 ∇GERM[⎕]∇
 ∇ R←X GERM Y;GER;QUAL
 GER←¯22.92+Y×2.61
 →(GER>0)/L1
 R←0
 →0
L1:→(GER<35)/L2
 GER←35
L2:QUAL←(¯140.3949+(58.1904×Y)+(¯8.1481×Y*2)+(0.3892×Y*
 3))÷35
 →(QUAL<1)/L3
 QUAL←1
L3:R←⌊X×(GER÷100)×QUAL×0.67×0.6
 →0
 ∇
```